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Breeding strategies for improving smallholder dairy cattle productivity in Sub-Saharan Africa

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Abstract

Breeding strategies for smallholder dairy farming systems in Sub-Saharan Africa (SSA) were simulated and evaluated considering cow traits identified as priorities by farmers in different agro-ecological zones. These traits were related to cow milk yield, fertility, temperament, feed intake and disease resistance. The first breeding strategy was based on continuous importation of genetically superior exotic dairy sire semen to SSA and crossing with local females leading to a gradual upgrade of the indigenous population. The second strategy assumed that semen from elite exotic bulls would be imported to SSA and used on indigenous cows to produce F1 animals. Thereafter, elite animals would be selected from within the F1 and each subsequent generation to establish a new synthetic breed. The third strategy was to improve the indigenous population by genetically selecting the best sires available domestically. Results showed positive genetic progress for all breeding goal traits. After 15 generations of selection, the genetic response of the importation strategy exceeded the corresponding genetic response of the synthetic breed strategy by 20%–60%. The former also exceeded the genetic response of the indigenous breed improvement strategy by 43%–75%. Potentially there is an opportunity for breeders to choose an appropriate breeding strategy that fits a specific need of smallholder dairy farmers.

KEYWORDS

breeding goal trait, breeding strategies, selection, smallholder dairy cattle

1 | INTRODUCTION

Earlier research was undertaken in Sub-Saharan Africa (SSA) has confirmed that the rate of genetic improvement for milk yield from indigenous breeds is low, ranging from 0% to 0.15% per year (Galukande et al., 1962; Mahadevan

et al., 1962; Marshall et al., 2019). The indigenous and exotic dairy breeds have been often crossed in unsystematic ways to produce a mixture of cattle of varying genetic composition (Mujibi et al., 2019). Because of the lack of clear crossbreeding and selection strategies, the resulting performance of the crossbreds has been most unpredictable (Cunningham

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& Syrstad, 1987), although the F1 crosses have been usually considered superior to the local breeds. However, upgrading to higher grade exotics has been viewed as compromising animal fitness and adaptability and often less economical than either generating F1 or improving indigenous ecotypes (Singh, 2015).

Routine genetic evaluations and selection of the best animals according to the breeding goal is not a common practice for most countries in SSA (Opoola et al., 2019). Breed preference has been often used as a guide for choosing breeding dairy cattle instead of individual animal selection based on a well-defined breeding goal with relevant animal traits. Performance of F1 crosses reportedly depends on the type of exotic breed used and the quality of breeding bulls selected within a breed (Vaccaro et al., 1999). For example, studies in the tropics have shown that Holstein-Friesian crosses offer the highest advantage for production traits while Jersey crosses have better fertility compared to the former (Singh, 2015).

Systematic crossbreeding programmes involving temperate and tropical breeds have demonstrated a considerable benefit when they are well planned (McDowell, 1985). Although crossbreeding has been adopted in SSA for more than one century, the smallholder dairy sector, which comprises the majority of dairy farmers, has not been able to achieve the desired gains. The major limitation includes lack of clear breeding strategies, mismatch of genotypes and environment, and lack of farmer participation in designing the breeding programmes (Galukande et al., 2013).

Serious efforts to improve the dairy industry in SSA countries such as Tanzania are currently underway (Michael et al., 2018; United Republic of Tanzania (URT), 2019). However, the success of genetic improvement would depend on the presence of a structured breeding programme focusing on animal traits identified by the farmers themselves (Chawala et al., 2019). Selection indices can now be developed, optimally combining these traits according to the agro-ecological zone and production system cattle are raised in (Chawala et al., 2019). Appropriate breeding strategies need to be defined based on these indices to underpin sustainable cattle genetic improvement in smallholder dairy farming in Tanzania and other parts of SSA.

The aims of the present study were to investigate alternative breeding strategies for dairy cattle genetic improvement and determine genetic progress for preferred animal traits identified by farmers in smallholder dairy production systems in SSA. Three breeding strategies for genetic improvement were developed and evaluated; (a) continuous importation of superior exotic sire semen, (b) formation of a new synthetic breed with repeat crossbreeding, (c) genetic improvement of indigenous populations based on the domestic selection of indigenous sires.

2 | MATERIALS AND METHODS

2.1 | Breeding goal traits and selection indices

Five animal traits identified previously by Chawala et al. (2019) as SSA dairy smallholder farmer-preferred traits were considered (Appendix 1). Additional animal traits from the dairy breeding programme in an exporting country, modelled here by the United Kingdom (Agriculture and Horticulture Development Board (AHDB), 2018; Interbull, 2019; Pritchard et al., 2013; Wall et al., 2005) were also included (Appendix 2). Three multi-trait selection indexes considering different trait combinations and differing amount emphasis for smallholder breeding goal traits were created: (a) Overall Farmer index: comprising the five SSA farmer-preferred traits (Chawala et al., 2019); (b) Reduced Farmer index: including the two most important and probably easiest to record SSA farmer-preferred traits; (c) Exotic index: combining all traits that are included in the exporting country selection index. The relative emphasis placed on each trait in the first two indices was from Chawala et al. (2019). In the exotic index, traits were combined according to AHDB (2018) and Interbull (2019). All selection indices are summarised in Appendices 1 and 2.

2.2 | Breeding strategies

Three basic breeding strategies were investigated (Appendix 3), assuming non-overlapping generations and offspring remaining always in the maternal herd with no cow movement between herds.

The first strategy (Strategy A) reflected a systematic version of the currently prevailing approach in smallholder dairy farming systems. In this strategy, selected exotic bull semen was imported in each generation and used to breed, by Artificial Insemination (AI), a given proportion of the cows in the population chosen at random across all herds. This proportion depended on the degree of usage of AI, which is explained later. The remaining cows in the population were mated with local bulls chosen at random from the same herd as the cows. In the first generation of selection, this strategy led to a mixed population of F1 crosses (descendants of AI) and indigenous animals (descendants of matings with local bulls). In the subsequent generations, the same practice was followed, with selected exotic bull semen used to breed the same proportion of cows randomly chosen from the population and the remaining cows being mated with local bulls. This strategy led to a gradual replacement of the indigenous cattle population by the repeated importation and use of selected exotic bull semen. Within this first strategy,

four separate selection scenarios of imported semen were investigated: (a) selection of exotic bull semen based on the Overall Farmer Index of the five SSA farmer-preferred traits (Scenario A1), (b) selection of exotic sires semen based on a Reduced Farmer Index comprising the two most important and easiest to record traits (milk yield and calving interval) among the SSA farmer preferences (Scenario A2), (c) selection of exotic bull semen based on the Exotic Index (Scenario A3) and (d) random selection of exotic bulls (Scenario A4). This strategy assumed that the exotic population was also genetically improved in parallel based on Exotic Index selection.

The second breeding strategy (Strategy B) was the development of a new synthetic breed. In this strategy, the selection and importation of exotic bull semen took place only in the first generation based on the Overall Farmer Index (Appendix 1). This semen was used to breed with AI a given proportion of indigenous cows, depending on the AI scheme described below. As in Strategy A, the remaining cows were randomly mated to local bulls. In subsequent generations, no exotic bulls were imported, but bulls from the population were selected based on the Overall Farmer Index to breed with AI the same proportion of the cows in the population chosen at random across all herds. Again, the remaining cows in the population were mated with local bulls chosen at random from the same herd as the cow (Scenario B5).

The third breeding strategy (Strategy C) involved no importation of exotic genetic material. Instead, the strategy was set up to improve the indigenous population by selecting, in each generation, the best indigenous bulls based on the Overall Farmer Index (Scenario C6) to breed with AI a proportion of the cow population chosen at random, with the remaining cows being mated to local bulls within the herd.

2.3 | Simulation study for the evaluation of breeding strategies

A semi-stochastic simulation was designed to determine the effectiveness of each breeding strategy based on predicted genetic and phenotypic progress from a genetic selection. Exotic and SSA indigenous cattle populations, each comprising 2,000 animals (50% males, 50% females) were simulated for this matter. The SSA indigenous population was distributed in 20 villages each with a herd size of 100 animals. Here, herd size was chosen to mimic a cohort of animals with expected panmictic reproduction. As such, this size reflects a group of animals raised in the same village where smallholders share local animals for reproduction.

In all strategies, a bull selection intensity of 10% was assumed. Selected bulls were used to breed by AI a proportion of cows randomly chosen from the population across different herds. This proportion was determined by the AI scheme in place. Three such schemes were tested in the present study:

the first scheme assumed 30% of the cows being AI bred, reflecting the current rate of AI uptake (Mwanga et al., 2019); the second assumed 50% suggesting an expected increase in AI uptake in the near future (African Dairy Genetic Gains, 2017); the third assumed all cows were bred with AI, portraying a 100% AI uptake as the long-term goal (Michael et al., 2018; the United Republic of Tanzania, 2019). Random allocation of cows to AI serving was assumed to mimic farmers joining or leaving the AI scheme in each generation. In all cases, offspring remained in the maternal herd.

Each breeding strategy was simulated for 15 generations of sire selection in 10 replicates each.

2.3.1 | Simulation of true breeding values and environmental values

True breeding values (TBVs) and environmental values (ENVs) of each animal trait were first simulated from multivariate normal distributions $MVN \sim (0, G_0)$ and $MVN \sim (0, E)$, respectively, where G_0 and E were the corresponding genetic and environmental variance-covariance matrices. Genetic variance estimates of traits in both populations were obtained from the literature as indicated in Appendix 4. Genetic correlation estimates among different traits were also obtained from the literature and assumed to be the same in both populations and environments (SSA and exotic). Genetic correlations between the exotic and SSA environment for the same trait were obtained from Interbull (2019) and pertained to correlations between the Republic of South Africa and the United Kingdom, which were used as a proxy for SSA and exotic environments, respectively. South Africa was chosen because it is the only country in SSA participating in the genetic evaluation of Interbull. All genetic correlations considered in the present study are summarised in Appendix 5. Genetic covariances among different traits and covariances for the same traits between the exotic country and SSA were calculated from the corresponding genetic correlations and genetic variances.

Phenotypic and environmental variances for each trait were calculated from the corresponding genetic variance and heritability estimates. Environmental covariances among traits were assumed to be zero.

2.3.2 | Simulation of estimated breeding values

Subsequently, estimated animal breeding values (EBVs) were generated independently for each trait based on TBVs, assuming a correlation between the two (accuracy of genetic evaluation, r) and a normal distribution $N \sim (0, r^2 \sigma_a^2)$, where σ_a^2 was the genetic variance of the corresponding trait. The accuracy of sire genetic evaluation was assumed to be based

on 100 daughters in the exotic breeding programme and 25 in SSA. In the present study, the accuracy of sire genetic evaluation was equivalent to the accuracy of selection and was calculated according to Oldenbroek and Waaij (2015).

2.3.3 | Simulation of phenotypes

The phenotype y of animal i was simulated for each trait and environment by adding the phenotypic mean (μ) to the TBV and ENV of the animal, as follows:

$$Y_i = \mu + \text{TBV}_i + \text{ENV}_i$$

Phenotypic means of all farmer-preferred traits in the exotic and SSA indigenous populations were obtained from the literature (Ayalew et al., 2015; Ilatsia et al., 2007; Interbull, 2019; Ojango & Pollott, 2001; Opoola, 2018; Pritchard et al., 2013; Wasike et al., 2009). Data on improved zebu, Sahiwal and Boran, cattle (Haile-Mariam & Kassa-Mersha, 1994; Ilatsia et al., 2007, 2011; Musingi et al., 2018; Wasike et al., 2009) were considered as inputs for the SSA indigenous breeds. Phenotypic averages are shown in Appendix 6.

2.3.4 | Selection and mating

The emphasis on animal traits identified by farmers as priority traits was used to determine the selection weight on individual traits in selection indices for smallholder dairy farmers. Additional selection indices for exotic bulls in their country of origin were considered, based on the exotic selection index (AHDB, 2018; Interbull, 2019). For each breeding strategy and scenario, individual trait EBVs were combined to form the corresponding selection indexes described in Appendices 1 and 2. Sires were then ranked based on the corresponding index value for each selection scenario and the top 10% were selected to randomly mate with cows and breed the next generation.

2.3.5 | True breeding values of offspring

In each generation following selection, TBVs of the offspring of two animals were estimated from the average TBVs of the parents plus an individual Mendelian sampling (MS) term to account for random sampling of parental alleles. Thus, TBVs of offspring were calculated as follows:

$$\text{TBV}_{\text{Offspring}} = 0.5 * (\text{TBV}_{\text{Sire}} + \text{TBV}_{\text{Dam}}) + \text{MS}_{\text{TBV}}$$

The Mendelian sampling term for TBVs followed a distribution $\text{MVN} \sim (0, 0.5(1 - \bar{F}) G_0)$, where \bar{F} is the average

inbreeding coefficient of the parents and G_0 is the variance-covariance matrix of the base population. For crossbred animals, G_0 was a combination of the genetic variance-covariance matrices weighted by the relative genetic composition emanating from the indigenous and exotic populations; hereafter this will be referred to as the proportion of genes from the respective populations. In all generations after the base population, ENV was simulated from $\text{MVN} \sim (0, E)$, with E being a mixture of the environmental variance-covariance matrices weighted by the proportion of genes from the indigenous and exotic populations.

2.3.6 | Evaluation of simulated selection scenarios

The means of animal TBV for all traits were estimated per generation, thereby providing estimates of predicted genetic progress under the different breeding strategies. The average proportion of exotic genes and level of inbreeding were also calculated per generation.

In addition, the effectiveness of each breeding strategy was further assessed based on phenotypic progress. In this case, individual phenotypes were derived for each generation and trait including estimates of heterosis and recombination loss. Heterosis and recombination loss were calculated for each crossbred animal based on the proportion of exotic genes for sire and dam. Estimates for the coefficients of heterosis (β_h) and recombination loss (β_r) for the crossbreds were calculated as follows (Dickerson, 1973; Wall et al., 2005):

$$\beta_h = P_S(1 - P_D) + P_D(1 - P_S)$$

$$\beta_r = P_D(1 - P_D) + P_S(1 - P_S)$$

where P_S and P_D are the proportion of exotic genes for the sire and dam, respectively. Afterwards, trait phenotype was calculated as follows:

$$\text{Phenotype} = \text{TBV} + \beta_h * \text{Max. } H + \beta_r * \text{Max. } R$$

where $\text{Max. } H$ = Maximum value for heterosis and $\text{Max. } R$ = Maximum value for recombination loss. The maximum values of heterosis ($\text{Max. } H$) and recombination loss ($\text{Max. } R$) for the breeding goal traits are presented in Appendix 7.

In all cases, results from each breeding strategy and selection scenario were averaged across 10 replicates.

2.4 | Sensitivity analyses

Three separate sensitivity analyses were carried out to assess the impact of changing input parameters on genetic and phenotypic progress.

2.4.1 | Sensitivity analysis I: Impact of different trait emphasis in the selection indices in agro-ecological zones

Chawala et al. (2019) indicated that farmer's trait preferences were influenced by different agro-ecological conditions and derived separate trait weights (emphasis placed on each trait) for the semi-temperate highland and the tropical coastal regions of Tanzania. These zones are described in detail in Chawala et al. (2019). Briefly, the former refers to the southern highland zone, with an altitude of 400–2,000 m, moderate temperatures, and seasonal rainfall from December to April. In contrast, the eastern coastal zone covers the coast belts and lowland areas and is characterised by high temperatures and bimodal rain patterns (February–May and October–December). In the present study, separate Overall Farmer Indexes, which were developed by Chawala et al. (2019), were assessed for these two agro-ecological zones.

2.4.2 | Sensitivity analysis II: Impact of reduced performance of the exotics in SSA

The assumed performance of exotics in SSA was further reduced by 25% compared to values in Appendix 6. Thus, the phenotypic mean for lactation milk yield (LMY) was reduced from 4,050 to 3,038 kg, calving interval (CI) increased from 462 to 578 days, temperament (TEMP) was reduced from 4.7 to 3.5 score, mature live weight (BWT) increased from 557 to 648 kg and longevity (LF) decreased from 2.68 to 2.0 lactations. Comparisons were then performed based on the predicted genetic progress of indices and individual breeding goal traits.

2.4.3 | Sensitivity analysis III: Impact of reduced fitness of the exotics in SSA and an antagonistic genetic correlation between production and fitness traits

The fitness and adaptability of dairy cattle tend to differ according to the environment. Furthermore, the genetic correlation between production and survival or fitness traits is often antagonistic. Therefore, the expected longevity of exotic cattle in SSA was further reduced by 25% and the genetic correlation between LMY and LF changed from zero (Appendix 5) to -0.34 according to Pritchard et al. (2013).

In all sensitivity analyses, comparisons were performed based on the predicted genetic progress of indices and individual breeding goal traits.

3 | RESULTS

3.1 | Population structure in different breeding strategies

Figure 1 shows the levels of exotic genes in the population across generations in the six breeding scenarios outlined above. Results pertain to 100%, 50% and 30% AI mating schemes. In the strategies of importation (upgrading) and synthetic breed formation, the rate of replacement of the indigenous population increased depending on the proportion of AI penetration. For example, the levels of exotic genes in all upgrading scenarios (A1, A2, A3 and A4; strategy A) at generation five were 96.9%, 76.4% and 55.5% for 100%, 50% and 30% AI schemes, respectively. When developing a new synthetic breed, the percentage of exotic genes varied depending on the proportion of the indigenous population involved in the formation of the foundation stock. The maximum percentage of exotic genes in the newly created synthetic breed was 50%, 31.1% and 18.5% for 100%, 50% and 30% AI mating schemes, respectively.

3.2 | Inbreeding level

The average inbreeding coefficient per generation for the six selection scenarios are shown in Appendix 8. The respective slopes (inbreeding increase per year) at 100% AI was 0.15% for scenarios A1, A2, A3, B5 and B6, and 0.14% for scenario A4. The corresponding slopes at 50% AI for scenarios A1, A2, A3, A4, B5 and C6 were 0.14%, 0.13%, 0.14%, 0.12%, 0.08% and 0.08%, respectively. Similar slopes were observed for the 30% AI scheme. However, there was a considerable difference at 50% and 30% AI schemes, where the rate of inbreeding was higher under the importation (upgrading) strategy compared to the other two.

3.3 | Predicted genetic progress in individual breeding goal traits

Genetic progress of the farmer-preferred traits in SSA for all six breeding scenarios are presented in Figure 2 and pertain to the 100% AI mating scheme. Corresponding results for 50% and 30% AI mating schemes considered in the present study are presented in Appendix 9.

Figure 2 demonstrates a clear difference in genetic trends of traits between the importation/upgrade strategy (selection scenarios A1, A2, A3, and A4), the new synthetic breed strategy (scenario B5) and the improvement of the indigenous population strategy (scenario C6). Genetic

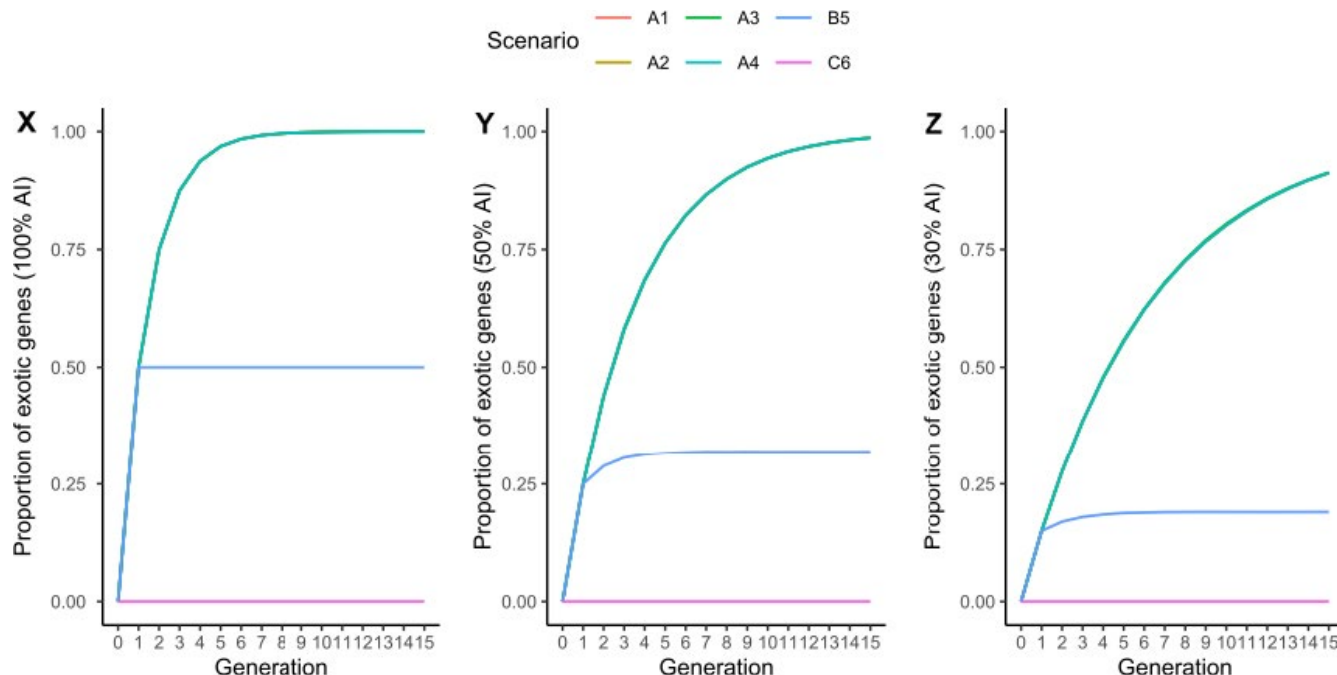


FIGURE 1 Proportion of exotic genes in six selection scenarios at 100% AI (X), 50% AI (Y) and 30% AI (Z) mating schemes. Scenarios A1–A4 pertain to imported exotic sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the overall farmer index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C)

trends in scenarios A1, A2, A3 were very similar. The genetic trend for scenario A4 lagged slightly compared to the other three scenarios under the importation/upgrade strategy.

Genetic progress for lactation milk yield (LMY), the most important trait according to farmer preferences (Appendix 1), was highest for the importation/upgrading strategy (scenarios A1, A2, A3, A4) compared to the other two strategies (scenarios B5, C6). The genetic trends of LMY for scenarios A1, A2 and A3 (all within the importation strategy) were very similar. Expectedly, scenario A4 (random importation of exotic sires) showed relatively lower genetic progress for LMY compared to scenarios A1, A2 and A3. At generation 15, the genetic progress for LMY in scenarios A1, A2, A3, A4 and B5 was 1.68, 1.70, 1.72, 1.59 and 1.32 times greater compared to scenario C6. Across 15 generations, the average phenotype for LMY in scenarios A1, A2, A3, A4, B5 and C6 increased by 5.97, 6.05, 6.10, 5.63, 4.75 and 3.55-fold, respectively, compared to the base generation.

Calving interval (CI), the second most important trait according to farmer preferences (Appendix 1), was predicted to increase slightly in all the six scenarios despite having a negative relative weight in all selection indexes because of its strong and unfavourable genetic correlation with production traits (0.45–0.47). Thus, the increase in CI reflected the selection emphasis placed on LMY in the various indexes. Notably, the genetic trends for CI show that there was a small

gap among the breeding strategies. Genetic trends of CI for scenarios A1, A2, A3 and A4 were relatively similar. At generation 15, the undesirable positive genetic trend for CI in scenarios A1, A2, A3, A4 and B5 was 1.04, 1.05, 1.05, 1.05 and 1.04 times greater compared to scenario C6. Across 15 generations, the TBV for CI in scenarios A1, A2, A3, A4, B5 and C6 had a 1.06, 1.07, 1.07, 1.06, 1.04 and 1.02-fold increase, respectively, compared to the base generation.

Genetic trend for temperament (TEMP) increased in the preferred direction in all breeding scenarios. The increase in TEMP was dictated by both a positive emphasis on the index and a favourable genetic correlation with milk production. The genetic progress for TEMP after 15 generations of selection in breeding scenarios A1, A2, A3, A4 and B5 was 0.95, 0.92, 0.90, 0.90 and 1.04 times greater compared to scenario C6. After 15 generations, the TBV for TEMP in scenarios A1, A2, A3, A4, B5 and C6 increased by 1.28, 1.24, 1.20, 1.20, 1.40 and 1.34 folds, respectively, compared to the base generation.

The genetic trends for the mature live weight (BWT) increased initially for breeding scenarios A1, A2, A3 and A4 (importation/upgrading strategy) because of a moderate positive genetic correlation with production traits (0.23–0.26) in the Exotic Index. There was no difference in genetic trends of BWT among scenarios A1, A2 and A3 but there was a considerable lag between them and scenario A4 (random selection in importation). At generation 15, the genetic increase for BWT in scenarios A1, A2, A3, A4 and B5 was 1.83, 1.87, 1.88, 1.85

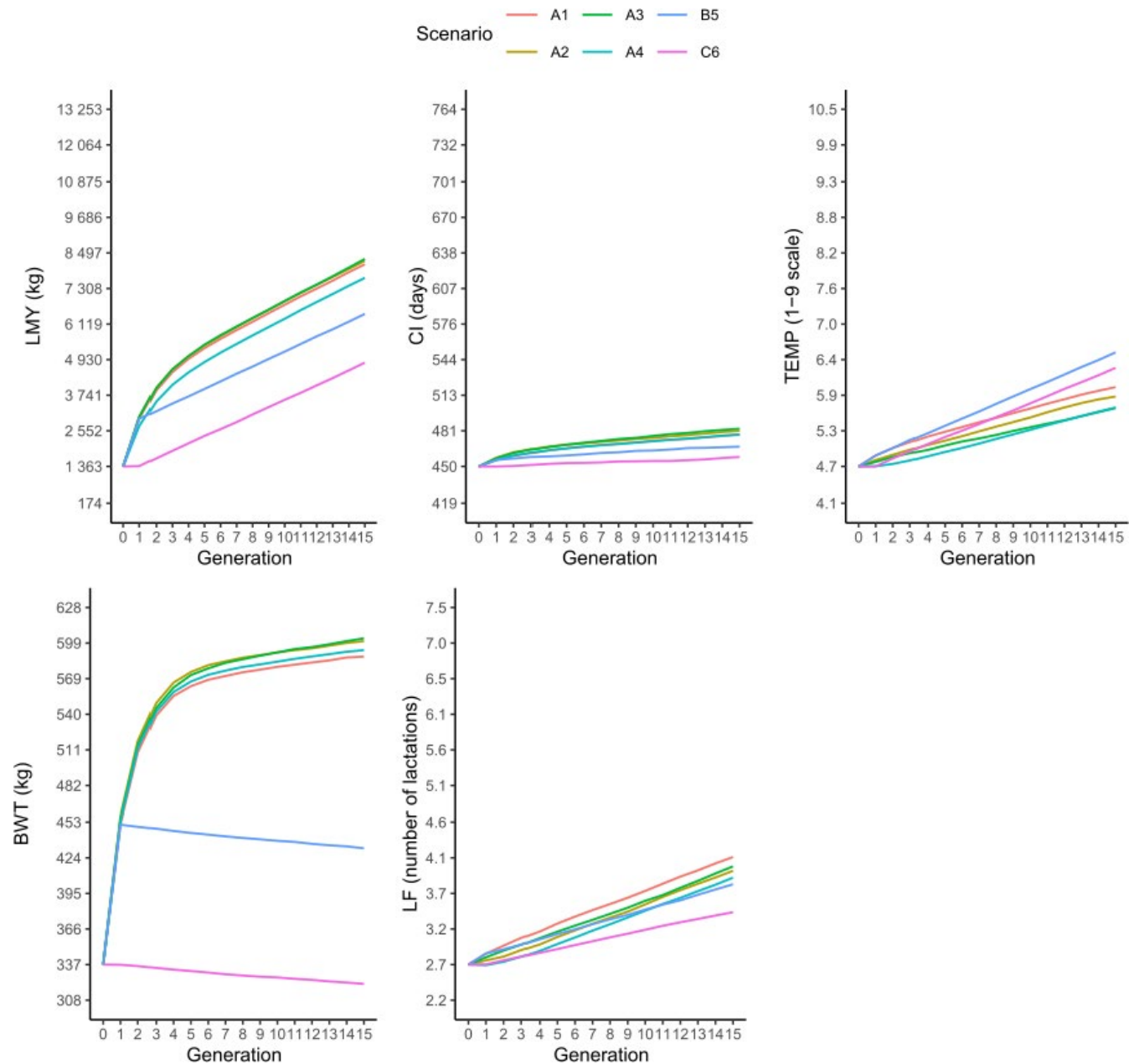


FIGURE 2 Predicted genetic progress per generation for six selection scenarios for 305-day milk yield (LMY), calving interval (CI), temperament (TEMP), mature live weight (BWT) and longevity (LF) in the 100% AI mating scheme. Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C)

and 1.34 times greater compared to scenario C6. After 15 generations of selection, the TBV for BWT in scenarios A1, A2, A3, A4, B5 and C6 increased by 1.74, 1.78, 1.79, 1.76, 1.28 and 0.95-fold, respectively, compared to the base generation.

Predicted genetic progress for longevity (LF) was in the intended direction in all breeding scenarios. Greater genetic progress for LF was seen in the importation strategy (scenarios A1, A2, A3 and A4) compared to the new synthetic breed (scenario B5) and indigenous improvement (scenario C6)

strategies. At generation 15, the genetic progress for LF in scenarios A1, A2, A3, A4 and B5 was 1.22, 1.16, 1.18, 1.14 and 1.11 times greater compared to scenario C6. After 15 generations of selection, the TBV for LF in scenarios A1, A2, A3, A4, B5 and C6 improved by 1.54, 1.47, 1.49, 1.43, 1.40 and 1.26 folds, respectively, compared to the base generation.

Table 1 summarises the genetic gain per generation for each trait under the different breeding scenarios and AI schemes. Overall, an increase in the proportion of AI penetration was

AI scheme	Selection scenario	LMY (kg)	CI (days)	BWT (kg)	LF (No. lactations)	TEMP (1–9 scale)
100%	A1	375.4	1.62	10.33	0.09	0.08
	A2	380.2	1.72	10.78	0.09	0.08
	A3	383.3	1.91	11.12	0.09	0.06
	A4	359.7	1.62	10.55	0.08	0.07
	B5	279.2	0.97	1.12	0.07	0.12
	C6	239.7	0.52	−1.09	0.05	0.11
50%	A1	389.2	1.68	13.77	0.08	0.08
	A2	395.4	1.85	14.41	0.08	0.07
	A3	397.3	1.93	14.57	0.08	0.06
	A4	364.6	1.66	13.99	0.07	0.06
	B5	158.9	0.38	1.61	0.04	0.07
	C6	135.3	0.27	−0.62	0.03	0.06
30%	A1	352.0	1.48	14.02	0.07	0.06
	A2	357.9	1.64	14.69	0.06	0.06
	A3	361.3	1.78	14.76	0.06	0.05
	A4	326.2	1.47	14.25	0.05	0.04
	B5	97.1	0.17	0.98	0.02	0.04
	C6	83.2	0.13	−0.42	0.02	0.04

Note: LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

favourable for LMY, LF and TEMP, while lower AI uptake was advantageous for BWT and CI. Appendices 10 and 11 present the rate of genetic gain separately for generations 1–5 and generations 6–15. Overall, the rate of genetic progress was higher in generations 1–5 (early selection) compared to generations 6–15.

Appendix 12 illustrates the predicted genetic progress of animal traits included in the breeding goal (exotic index) in the country of origin of exotic sires, which is relevant to the importation selection scenarios.

3.4 | Predicted genetic progress in the Overall Farmer Index

The genetic progress achieved in the six selection scenarios with regards to the genetic Overall Farmer Index is shown in Figure 3. The importation/upgrading strategy (scenarios A1–A4) ranked higher compared to the synthetic breed strategy (scenario 5) and indigenous breed improvement strategy (scenario C6). Genetic progress for importation scenarios A1, A2 and A3 were better than scenario A4. At generation 15 in the 100% AI scheme, the genetic progress in scenario A1 was 1.25 and 1.76 times greater compared to scenarios B5 and C6, respectively. Genetic progress was affected by the type of AI schemes and increased with the increasing percentage

TABLE 1 Average predicted genetic gain per generation and breeding goal trait, by selection scenario and Artificial Insemination (AI) scheme

of AI use. The highest AI rate (100%) narrowed the gap between the importation strategy on the one hand and synthetic breed and indigenous improvement strategies on the other.

3.5 | Predicted phenotypic progress in individual breeding goal traits

Predicted phenotypic progress (trends) for individual breeding goal traits assuming a 100% AI scheme is shown in Figure 4. In general, phenotypic progress after the first generation of selection for LMY, CI, BWT and LF were steeper than for genetic trends (Figure 2). This is attributed to the phenotypic performance of F1 being higher than the additive genetic merit due to maximum heterosis in the crossbred offspring. Phenotypic values of traits decreased in the first backcross (scenarios A1–A4) and F2 (scenario B5) due to the unfavourable effect of recombination loss. A desired direction of the phenotypic trends was observed in subsequent generations in response to continuing selection. LMY and LF increased while CI was reduced. The relatively flat trend of BWT from generation six and above reflects a stable mature live weight due to negative emphasis of BWT in the Overall Farmer Index. Appendix 13 illustrates predicted phenotypic progress of animal traits in 50% and 30% AI schemes.

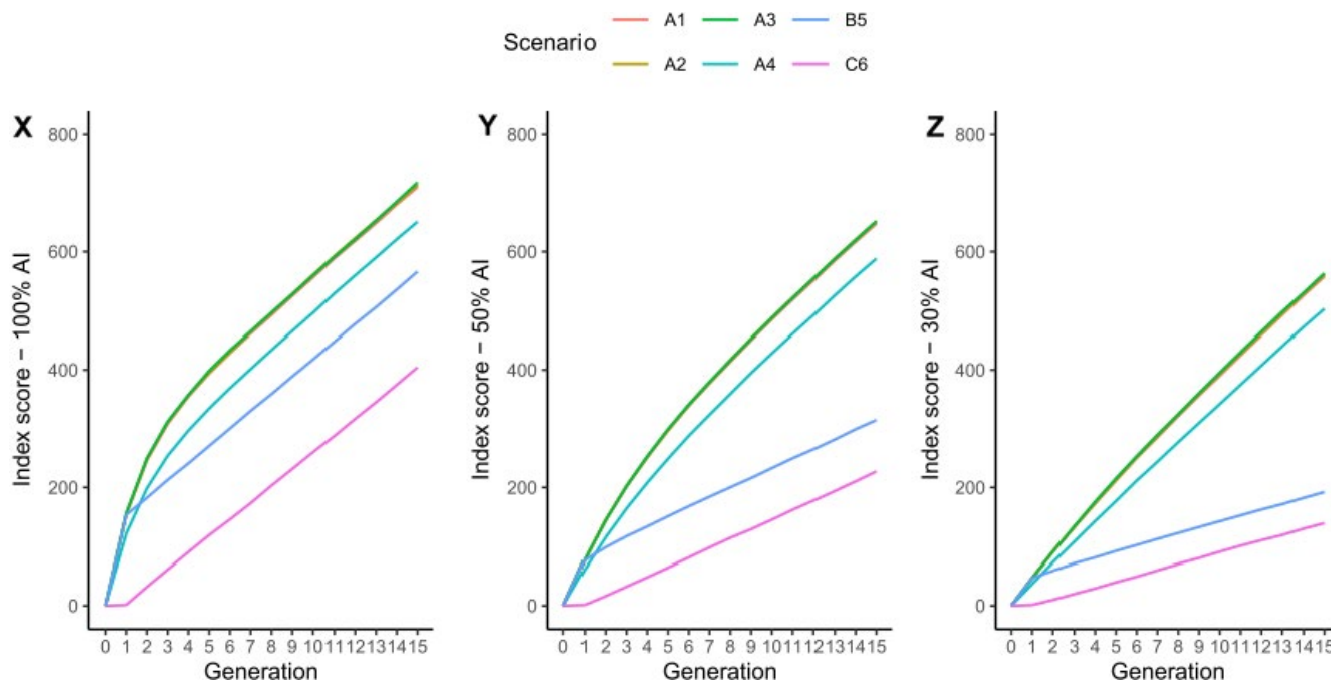


FIGURE 3 Predicted genetic progress per generation in the Overall Farmer Index for six selection scenarios assuming 100% (X), 50% (Y) and 30% (Z) AI schemes. Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C)

3.6 | Predicted phenotypic progress in the Overall Farmer Index

Figure 5 shows the predicted phenotypic progress for the phenotypic Overall Farmer Index under the six selection scenarios. Within the 100% AI scheme, the phenotypic progress for scenario A1 at generation 15 was 1.15 and 1.60 times better compared to scenarios B5 and C6, respectively. Higher predicted phenotypic progress was associated with a higher percentage of AI. As with genetic trends, differences in phenotypic performance between the importation strategy and the other two strategies increased with decreased AI uptake.

3.7 | Sensitivity analyses

3.7.1 | Sensitivity analysis I: Impact of different trait emphasis in the selection indices in agro-ecological zones

The predicted genetic progress in the Overall Farmer Index (Appendices 14 and 15) and individual breeding goal traits (Appendices 16 and 17) were calculated using different farmers' preference weights on animal traits in semi-temperate and tropical agro-ecological zones, respectively. In both zones, genetic progress under the importation

scenarios exceeded that of synthetic breeds and indigenous improvement strategies. The differences in genetic progress for animal traits and selection indexes between scenarios A1, B5 and C6 are shown in Table 2; selection under these scenarios is based on the Overall Farmer Index representing the three breeding strategies described previously. Sensitivity analysis showed that goal traits and selection indexes were sensitive to changes in preference weight based on agro-ecological zones. The advantages of importing exotic animals (strategy A) versus the other strategies were smaller in the semi-temperate zone than in tropical areas. For example, the difference in genetic progress based on the Overall Farmer Index between scenarios A1 and B5 in the tropical coastal zone at 100% AI (Table 2) was twice that in the semi-temperate highland zone. However, these differences were also dependent on the proportion of AI uptake and became smaller at lower levels of AI use. Relevant results pertaining to the individual animal traits are presented in Appendix 18.

3.7.2 | Sensitivity analysis II: Impact of reduced performance of the exotics in SSA

Reducing the performance of exotic breeds in SSA by 25% scenario affected predicted genetic progresses for individual

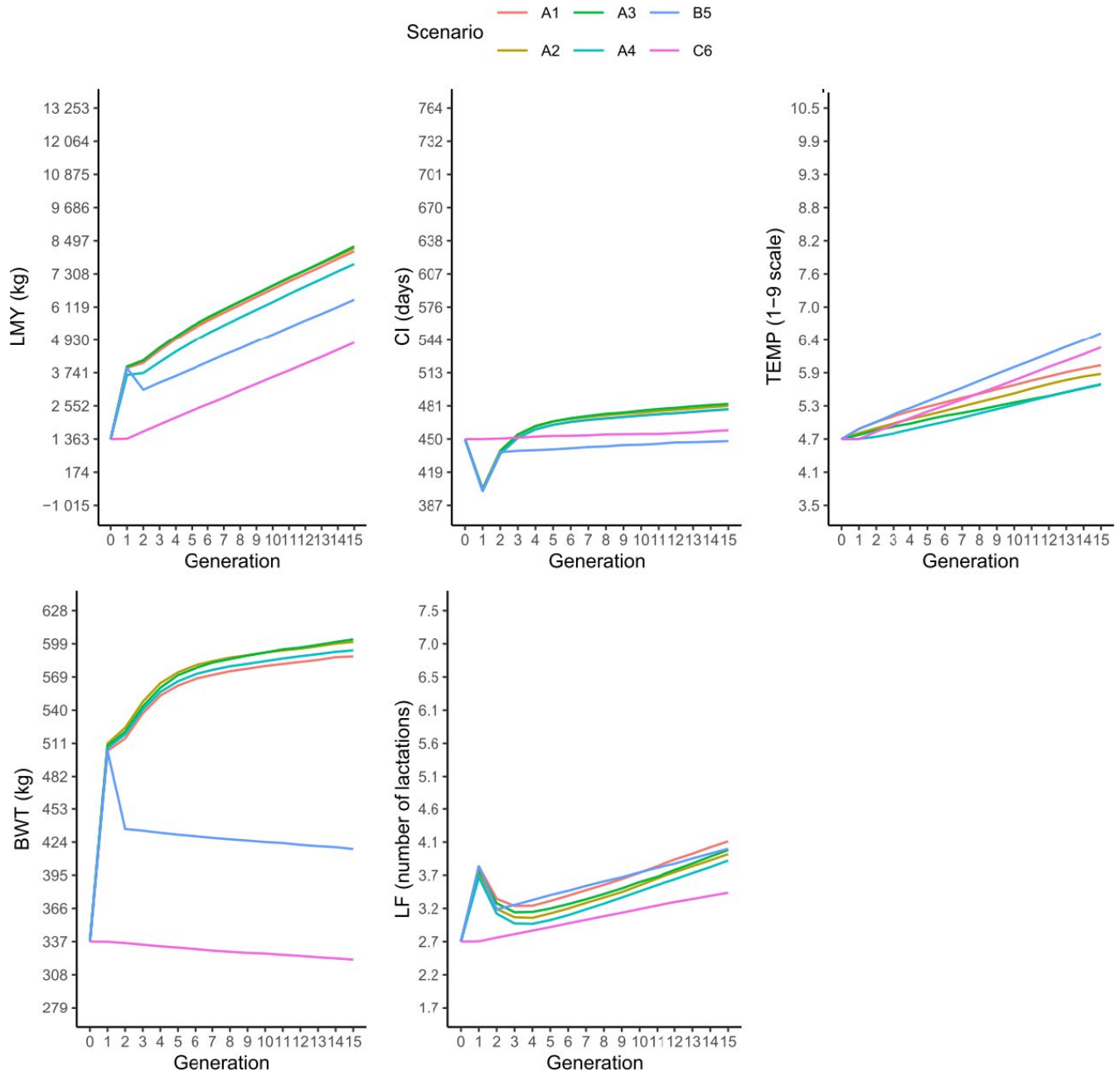


FIGURE 4 Predicted phenotypic progress per generation for six selection scenarios for 305-day milk yield (LMY), calving interval (CI), temperament (TEMP), mature live weight (BWT) and longevity (LF) assuming 100% AI mating scheme. Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C)

animal traits and the Overall Farmer Index. Table 3 shows the differences of predicted genetic progress in the index for breeding scenarios A1, B5 and C6 across and within agro-ecological zones. In general, the importation strategy still performed better compared to the new synthetic breed and indigenous cattle improvement strategies. Results for the individual animal traits and indexes are summarised in Appendices 19–25.

3.7.3 | Sensitivity analysis III: Impact of reduced fitness of the exotics in SSA and an antagonistic genetic correlation between production and fitness traits

When the average longevity of exotic dairy cattle was assumed to be reduced from 2.68 to 2.0 lactations and the genetic correlation with milk changed from zero to an

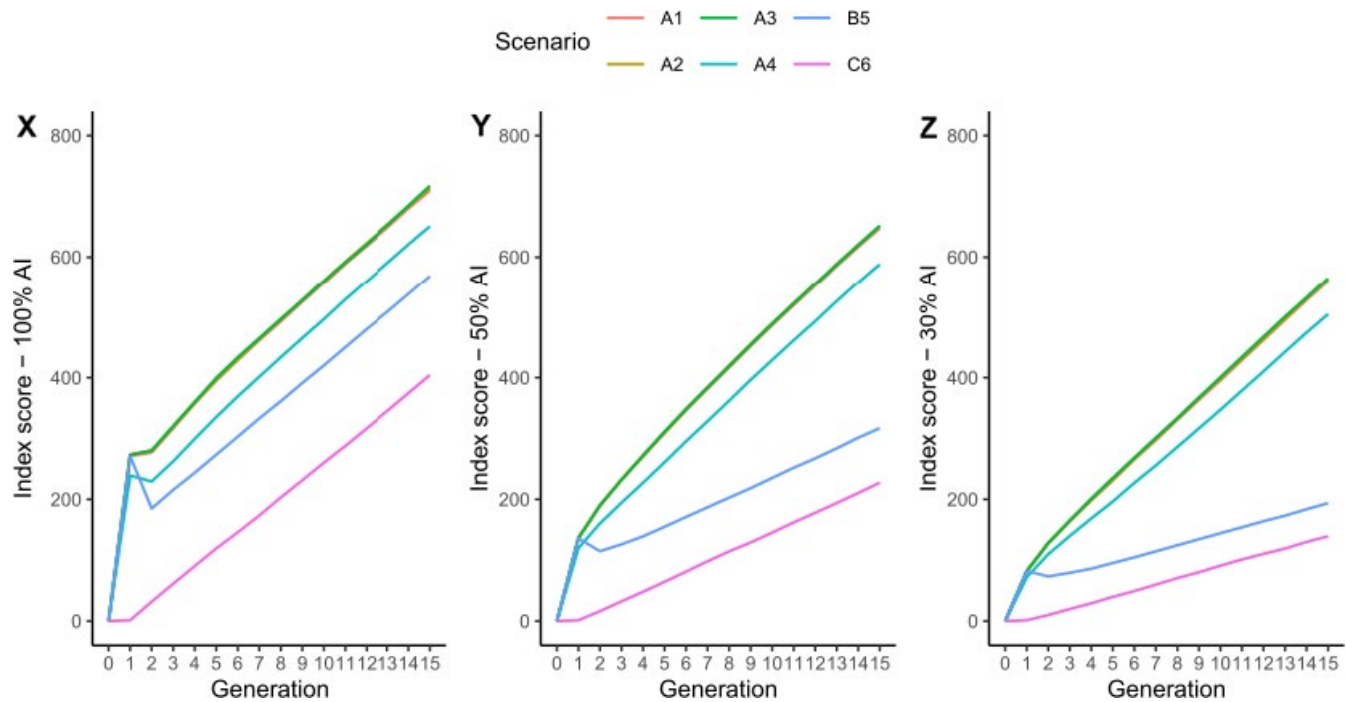


FIGURE 5 Predicted phenotypic progress per generation in the Overall Farmer Index for six selection scenarios. Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C)

TABLE 2 Relative differences (%) in predicted genetic gain in the Overall Farmer Index after 15 generations in semi-temperate and tropical zones between selection scenarios A1 (Importation strategy), B5 (Synthetic breed strategy) and C6 (Indigenous breed improvement strategy)

Type of index	AI scheme	Difference (%) of genetic gain between scenarios	
		Scenario A1 versus B5 ^a	Scenario A1 versus C6 ^a
Overall Farmer Index Semi-temperate zone	100%	14.66%	37.07%
	50%	47.02%	61.74%
	30%	61.99%	72.47%
Overall Farmer Index Tropical zone	100%	28.72%	39.78%
	50%	57.11%	69.47%
	30%	63.86%	73.27%

^aScenario A1 versus B5 = Relative difference (%) in genetic gain under scenario B5 in comparison to scenario A1; A1 versus C6 = Relative difference (%) in selection response under scenario C6 in comparison to scenario A1.

antagonistic -0.34 , the predicted genetic progress decreased for both the individual traits and the Overall Farmer Index. In addition, differences between breeding scenarios became smaller compared to the base simulation. Appendices 25–27 summarise results for individual traits and the Overall

Farmer Index. The differences in genetic progress for selection indexes between scenarios A1, B5 and C6 are shown in Table 4. Sensitivity analysis showed that Overall Farmer Index progress was affected by changes in the genetic correlation between production and fitness traits. Overall, the differences in genetic selection response between scenarios were smaller here compared to base simulation. For example, the difference in selection index response between scenario A1 and B5 in the base simulation was 20.26% (100% AI scheme) compared to 13.11% here.

4 | DISCUSSION

The overall aim of the present study was to investigate alternative dairy cattle breeding strategies for smallholder dairy farmers in SSA and identify the most appropriate strategy, which could be used as a guide for future dairy cattle breeding programmes. Results demonstrated that different levels of progress in dairy productivity may be achieved through sire genetic evaluation and selection. The study quantified the relative merit of three distinct breeding strategies: (a) upgrade of the indigenous population through systematic importation of exotic sire semen and crossing, (b) development of a new synthetic breed based on first-generation crossing between indigenous and imported exotics, and within

TABLE 3 Relative differences (%) in predicted genetic gain in the Overall Farmer Index after 15 generations of selection across and within agro-ecological zone between selection scenarios A1 (Importation strategy), B5 (Synthetic breed strategy) and C6 (Indigenous breed improvement strategy); performance of exotic sires in sub-Saharan Africa was assumed to be reduced by 25% compared to the base simulation design

Type of index	AI scheme	Difference (%) of genetic gain between scenarios	
		Scenario A1 versus B5 ^a	Scenario A1 versus C6 ^a
Overall Farmer Index	100%	10.70%	24.74%
Overall (across zones)	50%	47.59%	52.35%
	30%	61.11%	65.18%
Overall Farmer Index Semi-temperate zone	100%	5.93%	19.86%
	50%	44.62%	50.97%
	30%	58.91%	64.35%
Overall Farmer Index Tropical zone	100%	19.75%	28.39%
	50%	52.09%	54.97%
	30%	63.51%	65.84%

^aScenario A1 versus B5 = Relative difference (%) in selection response for scenario B5 in comparison to scenario A1; A1 versus C6 = Relative difference (%) in selection response for scenario C6 in comparison to scenario A1.

TABLE 4 Relative differences (%) in predicted genetic gain in the Overall Farmer Index after 15 generations of selection between scenarios A1 (Importation strategy), B5 (Synthetic breed strategy) and C6 (Indigenous breed improvement strategy); an antagonistic correlation between animal production and fitness (longevity) was assumed combined with reduced fitness of the exotics in sub-Saharan Africa

Type of index	AI scheme	Difference (%) of genetic gain between scenarios	
		Scenario A1 versus B5 ^a	Scenario A1 versus C6 ^a
Overall Farmer Index	100%	13.11%	37.57%
	50%	48.24%	62.16%
	30%	63.60%	72.89%

^aScenario A1 versus B5 = Relative difference (%) in selection response for scenario B5 in comparison to scenario A1; A1 versus C6 = Relative difference (%) in selection response for scenario C6 in comparison to scenario A1.

generation selection thereafter, and (c) genetic improvement of the indigenous population based on domestic selection. Selection criteria in different selection scenarios included an Overall Farmer Index, a Reduced Farmer Index and an Exotic Index. All breeding strategies and selection scenarios were assessed based on the genetic and phenotypic progress of the Overall Farmer Index and its constituent traits, which constitute the top SSA smallholder farmer preference as previously described by Chawala et al. (2019).

4.1 | Genetic and phenotypic progress

The breeding strategy based on the importation of exotic sire semen and crossing with cows locally was superior with regards to genetic and phenotypic progress of the Overall Farmer Index. All four selection scenarios within this strategy ranked higher compared to the synthetic breed and indigenous breed improvement strategies. As expected, amongst the four importation scenarios, selection on the Overall Farmer Index was the best and random selection was the least successful. After 15 generations of selection, the genetic gains from continuous importation of animals based on the Overall Farmer Index were 8%–10% higher compared to randomly importing from the country of origin of exotic sires. The superiority of the importation breeding strategy compared to the synthetic breed and indigenous breed improvement strategies may be attributed to the high relative emphasis on milk yield placed by the smallholder farmers combined with the considerable superiority of the exotic population with regard to this trait. This remained the case even when the performance of the exotics in SSA was assumed to be quite low in the sensitivity analyses performed within the present study. Additionally, the importation strategy benefited from parallel genetic selection and improvement in the country of origin of the exotic sires.

Results showed positive genetic progress for the individual breeding goal traits over generations in all three breeding strategies. Increasing the proportion of cows bred by improved sires through artificial insemination (AI) resulted in greater genetic progress in all selection scenarios.

The effect of heterosis was in the desirable direction for all traits manifested by increased lactation milk yield (LMY), shorter calving interval (CI), reduced mature live weight (BWT), increased longevity (LF) and better temperament (TEMP) in the F1. Phenotypic performance declined in crossbreds in subsequent generations compared to the F1 due to recombination losses. Nevertheless, positive phenotypic trends continued to be observed due to the impact of genetic selection. A detailed discussion of the genetic and phenotypic progress for individual breeding goal traits is provided below; traits are discussed in order of priority in the African Overall Farmer Index (Chawala et al., 2019; Appendix 1).

4.1.1 | Lactation milk yield (LMY)

Milk has been considered as the principal source of protein and income for smallholder dairy farmers in SSA (Salami et al. 2010; Somda et al. 2005). The results from the present study show a substantial genetic progress for milk yield in all breeding strategies considered because LMY was the most emphasized upon trait in the Overall Farmer Index. Indeed, the relative weight of LMY in the index was twice

compared to CI, TEMP and BWT, and three times compared to LF (Chawala et al., 2019). Therefore, results demonstrate the potential of selectively breeding for high milk yield in smallholder dairy production systems. The large difference in LMY assumed between the exotics and the indigenous cattle populations was the main factor for the success of the importation strategy over the synthetic breed and indigenous improvement strategies. In addition, the heritability of LMY was greater compared to other traits in all production environments. The synthetic breed strategy resulted in lower LMY compared to importation but was still competitive especially in semi-temperate conditions due to the use of selected crossbred sires. Overall, the genetic trends for LMY in the different breeding strategies were positive indicating the impact of selection of the best sires in every generation.

The phenotypic trend for milk depicted the superiority of F1 crosses of exotics with indigenous cattle in all crossbreeding strategies. A decline in performance observed after the F1 generation was the result of breaking favourable ancestral gene combinations due to Mendelian segregation and independent assortment (Dickerson, 1973; Rutledge, 2001).

Large heterosis reported between *Bos taurus* and *Bos indicus* can also be explained by the large genetic divergence between the two populations (Lin et al., 2010; Loftus et al., 1994; Syrstad, 1985). Previous studies have concluded that the optimum proportion of milk production in tropics is achieved for crosses with about 50% exotic genes (Cunningham & Syrstad, 1987). The synthetic breed strategy led to this gene composition in the present study when 100% AI scheme was adopted. Galukande et al. (2013) reported the LMY for 50%–75% *B. taurus* crossbred dairy cattle in the tropics being 2.2–2.7 times higher than that of the indigenous *B. indicus*. However, further increasing the proportion of exotic genes resulted in lower milk yield compared to crossbreds with 50% *B. taurus* genes. Rutledge (2001) highlighted that the decrease in performance in the F2 is a result of recombination loss and not because of poor breeding programme designs. Superiority of LMY in the subsequent generation observed in the present study was mainly due to the advantage of using selected sires from the previous generations.

4.1.2 | Calving interval (CI)

Short CI highlights improved cow fertility and is important for increased length of productive life, income, lifetime profit and overall genetic progress (Do et al., 2013). Long CI decrease a cow's lifetime productivity, cause shifts in calving patterns and increase the chances of animal culling (Olori et al., 2002). The present study showed a small genetic change (increase) in the undesired direction for CI. This was mainly due to the positive (unfavourable) genetic correlation between CI and LMY suggesting that selection emphasis on

increased milk yield would result in longer calving intervals. The importation breeding scenarios led to longer CI due to higher milk production compared to the synthetic breed and indigenous improvement scenarios. In addition, CI has a relatively low heritability suggesting that the trait could be improved faster by parallel changes in herd management practices.

Mungube et al. (2019) reported an estimated loss of about US\$40 million due to long calving intervals of 450–500 days in Kenya's dairy industry. In the present study, we could expect reduced profitability for the importation breeding strategy because of relatively longer calving intervals compared to the other strategies. The economic losses due to longer CI could be minimised by building capacity for accurate heat detection, improved feeding, and regular check-up for reproductive diseases.

Recording of CI requires relatively little data collection, just consecutive calving dates. However, one of the drawbacks of CI is that the relevant records become available in later stages of the cow's production cycle compared to other measures of fertility traits. This drawback may be overcome by the use of genomic breeding values. Future considerations of traits affecting fertility in early stages of life and production cycle such as age at first calving, non-return rate in heifers, number of services per conception and days open would be warranted, but solid recording practices need to be in place.

4.1.3 | Temperament (TEMP)

Results showed that selection for cow TEMP, the third most important trait in the Overall Farmer Index, was advantageous for crossbred cattle in Africa. For lack of literature data, cow temperament level was assumed to be the same in the base generation of selection in both the exotic and indigenous populations. Therefore, any difference in TEMP between breeding strategies was mainly due to the AI scheme adopted, relative weight in the trait in the selection index, and genetic correlation with the other traits. Interestingly, the importation strategy led to better TEMP than synthetic breed and indigenous improvement strategies at the 50% and 30% AI schemes. Our results showed that increasing the AI uptake to 100% led to increased TEMP in the synthetic breed and the indigenous population mainly due to the high relative emphasis of TEMP in the Overall Farmer Index compared to the Exotic Index, where genetic improvement of the exotics in the country of origin was based on.

The relationship between temperament and life-time production efficiency in dairy cattle has been previously investigated (Haskell et al. 2014; Neja et al. 2015) revealing a positive correlation between TEMP and LMY. This implies that calmer cows will increase farm productivity and profitability. TEMP is also important for human safety at

milking and during handling. Chawala et al. (2019) associated preferences for docile cows in smallholder dairy farmers in Tanzania with the use of family labour in feeding, milking, health management and breeding of the animals.

4.1.4 | Mature live weight (BWT)

BWT was used here as a proxy to feed intake. Low feed intake was the fourth priority animal trait in farmer preferences (Chawala et al., 2019). Upgrading the indigenous cattle with exotic sire importation and crossing resulted in heavier cows. The large difference in BWT between the exotics and the indigenous cattle populations was the main factor for the heavier cows in the importation strategy over the synthetic breed and indigenous improvement strategies. Despite a negative weight for BWT in the Overall Farmer Index, BWT increased because of its positive genetic correlation with milk yield (Pérez-Cabal & Alenda, 2003), and the greater positive emphasis placed on the other and the higher LMY heritability. Thus, the importation breeding strategy resulted in the most productive cows but with heavier mature live weight.

Heterosis effects on BWT were greatest for the importation breeding strategy. In practice, high heterosis for BWT is undesirable because of the negative emphasis on BWT and feed intake. BWT in the synthetic breed was lower because of negative selection and high recombination loss in generations after the F1 generation due to *inter se* mating. This means that the importation strategy would produce cows with increased feed requirements, whereas the other strategies would result in lighter cows with low feed requirements.

When addressing the relationship of BWT with other traits, fertility of heifers is often related to mature live weight (Freetly et al., 2011). A delayed growth towards mature live weight means a prolonged age at the first service of breeding heifers. Also, calving problems are often associated with a low live body weight of the dam, especially in crossbreeding schemes with larger exotic cattle. Studies have shown that increasing live body weight at calving was associated with increased milk production for the first lactating cows (Bazeley, 2016; Moran, 2012). On the other hand, heavier animals had higher maintenance requirements for growth and milk production (Moran, 2012). Due to small land areas for growing fodder and long dry seasons, smallholder dairy farmers in SSA do not have enough feed resources for large heifers and cows. Therefore, breeding for smaller heifers in SSA is justified. Exotic high-grade dairy cattle with higher BWT are expected to perform better in semi-temperate areas, where the climate is cooler. Chawala et al. (2020), highlighted the importance of growing improved pastures and promoting recycled food waste and by-products as a way of assuring feed availability all year round in smallholder dairy systems.

4.1.5 | Longevity (LF)

This trait was considered here as a proxy for cow fitness and disease resistance, which was the fifth priority trait identified by smallholder farmers (Chawala et al., 2019). The disease is often the key reason for involuntary culling, leading to a shortened productive life and, hence, reduced longevity. Longevity is currently being considered in breeding goals for dairy cattle worldwide (Interbull, 2019). The heritability of the trait is often low (Kern et al., 2014; Musingi et al., 2018). In addition, an unfavourable genetic correlation between the longevity and production traits such as milk, fat and protein has been reported (Pritchard et al., 2013). In the present study, we demonstrated that a combination of selection and crossbreeding (Strategy A) may lead to higher genetic gains for longevity in dairy cattle raised in SSA. The genetic progress for LF was higher for the importation breeding strategy. Crossbreeding combined with selection will increase the number of lactations completed (productive longevity). Selection for LF ensures an increase in overall production performance without compromising animal fitness. Number of lactations completed was chosen here for consistency between the Overall Farmer Index and the Exotic Index. Also, this is an indicator of efficiency since an increase in number of lactations completed translates to increased milk production and income for the farmer.

The phenotypic progress in the present study showed that LF in the synthetic breed was relatively similar to upgrading via importation. Overall, the phenotypic trend for longevity was positive indicating that all studied breeding strategies would improve the longevity of dairy cattle in SSA.

4.2 | Impact of artificial insemination (AI) uptake on genetic and phenotypic progress

A higher proportion of AI uptake resulted in a greater genetic and phenotypic progress across all breeding strategies. This was due to an increase in the proportion of local cows mated with selected sires contributing towards the improvement of the breeding goal. In general, increasing the proportion of AI in the breeding population narrowed the differences between strategies. Interestingly, adoption of 50% AI may result in a relatively high proportion of genetic gains achieved by 100% AI adoption, especially under the importation/upgrade strategy. As AI uptake increased, the genetic progress increased up to a point followed by a plateau. This explains the high genetic progress for LMY, CI and BWT at 50% AI (Table 1) due to the admixture of population of animals with different levels of exotic genes. The impact of heterosis and recombination loss was larger for scenario B5 (Strategy B, formation of new synthetic breed) and scenario A4 (Strategy A, importation based on random sire selection) compared to

scenarios A1, A2 and A3 (Strategy A, importation based on genetic selection). Recombination loss in the ensuing generations resulted in a decreasing phenotypic trend in some scenarios when AI was 100%. After generation 3, the direction of the Overall Farmer Index was positive and favourable due to continuing genetic selection. In general, increasing the proportion of cows that are bred with elite selected bulls contributed to increased predicted genetic and phenotypic gains.

AI services have been established as a way of harnessing the genetic potential of elite exotic sires based mainly on genetic evaluation programmes in the country of origin. However, the coverage of AI for most countries in SSA is low and variable. A recent study by Mwanga et al. (2019) reported AI utilisation in 13.46%, 31.46%, 50.35% and 56.50% of the dairy cattle in Uganda, Tanzania, Ethiopia and Kenya, respectively. In the present study, we demonstrated how predicted genetic gain may increase by increasing the proportion of cows that are bred with elite selected bulls. As expected, the success of the studied breeding strategies would depend on improved AI uptake in combination with a systematic breeding programme being in place.

4.3 | Implications of proportion of cows participating in a breeding programme and agro-ecological zone on genetic progress

The genetic progress for individual goal traits and the Overall Farmer Index varied depending on the agro-ecological zone cattle were raised in. The importation and synthetic breed strategies led to better results in semi-temperate compared to tropical conditions. Nevertheless, the importation strategy was better than the other two in both agro-ecological zones. LMY for exotics was 5.8 times high compared to the indigenous population in the base generation (i.e. before selection started). These findings broadly support previous studies in this area linking the high productivity of animals in semi-temperate zones with favourable climate compared to the tropical zones (Chagunda et al., 2004). Dairy cattle with an increasing proportion of exotic genes are generally considered less adapted to tropical conditions and, therefore, some level of management and environmental modification need to be made to counter-balance this effect and increase productivity. This means that importation would be less superior to the other two strategies in the tropical zone compared to the semi-temperate. For example, improved housing and feed availability would keep the high-grade exotic dairy cows reasonably healthy and productive. This, however, could be costly and is unrealistic in some situations. Non-upgrading strategies (synthetic and indigenous improvement) may be promoted in tropical areas where the production environment is less favourable for the upgrades. The economic benefits of a synthetic breed over upgrades and indigenous breed in

smallholder systems has been reported in many regions of the tropics (Galukande et al., 2013). The new synthetic breed strategy could, for example, start by targeting the smallholder production systems in tropical zones where milk yield and fertility traits are equally important (Chawala et al., 2019).

4.4 | Inbreeding

The rate of inbreeding in all breeding scenarios studied was low, with an increase of 0.08%–0.14% per generation. Trends in inbreeding reached a maximum of 2% per generation after 15 generations of selection. These findings are consistent with Chagunda et al. (2018) who reported an average inbreeding of 0.8% among the smallholder dairy cattle population in Rwanda.

The breeding strategies assessed in the present study are not expected to compromise the level of genetic diversity in the SSA cattle population. The rate of inbreeding in the indigenous and crossbred populations was low because of systematic genetic improvement using imported sires, replacement of bulls in every generation, and random mating. Nevertheless, caution is recommended when integrating the chosen breeding strategy into prevailing local practices. Some of the latter need to be revised for optimal implementation of the new strategies. Some important current practices that may fall into this category are: (a) many countries in SSA have a limited number of bulls that are kept in AI centres and used for AI service for many years without being replaced; (b) inseminators and smallholder dairy farmers are inclined towards using the semen from few sires of high-yielding breeds such as Holstein, which are kept in these AI centres; (c) in areas where AI is limited, a single bull may be used to serve one or two villages for a long period without replacement; (d) coordinated platforms for systematic pedigree and record keeping of dairy cattle in smallholder systems are often missing and relevant infrastructure needs to be developed.

4.5 | Practical implementation

There are over 356 million cattle in Africa (FAOSTAT, 2019) of which the majority are indigenous breeds. The latter are diverse with unique genetic attributes and play a significant role in poverty alleviation and improving the livelihoods of the rural farmers in sub-Saharan Africa. The indigenous cattle breeds are a principal source of milk and in addition have a role in many socio-cultural functions such as marriage, or religious ceremonies (Anderson, 2003). However, the current commercial production trends, tend to focus on a few high-yielding breeds.

The present cow population in Tanzania is estimated at 7,444,213 million, of which 7,206,696 are indigenous cows

and 237,517 are non-indigenous upgrades and dual-purpose cows (National Bureau of Statistics (NBS), 2015). The target is to increase improved dairy cattle numbers by about 3.8 times from the current cattle population of 783,000 to 2,985,000 by 2021/2022 (Michael et al., 2018; United Republic of Tanzania (URT), 2019) in order to achieve the overall objective to establish a sustainable and competitive dairy sector. Recently prepared policy documents including the Tanzania Livestock Master Plan (Michael et al., 2018) and National Livestock Research Agenda 2020–2025 (United Republic of Tanzania (URT), 2019) highlight the importance of the dairy sector in poverty reduction, improved food security and increased national income. Currently, the government, international organisations such as International Livestock Research Institute and Heifer International, and local smallholder dairy farmers are focussing on increasing milk yield with the aim to reduce the production–consumption gap, which, under the current practice, is estimated to increase to 5.8 million litres over the next 15 years (Michael et al., 2018). This increase will be driven by increasing human population, income, and urbanisation. Similar trends are observed and documented across several countries in SSA (Shapiro et al., 2015, 2017). Results from the present study are expected to underpin the established livestock policies and government efforts to improve the dairy sector. The potential benefits and practical implementation of using imported purebred exotic, locally available crossbred and indigenous bulls for improving dairy productivity is discussed next.

Results of the present study showed that an importation breeding strategy will offer a significant improvement in dairy productivity. Systematic crossbreeding and selection based on farmer-preferred traits (Chawala et al., 2019) will lead to an overall better performance under the smallholder production systems compared to establishing a new synthetic breed or improving the indigenous population with domestic selection. The upgraded crossbreds will have better performance in terms of milk yield, longevity, and temperament. Systematic gradual upgrading will allow time for the foreign genotypes to be adapted to the local conditions. However, this strategy will also result in animals with heavier bodyweight, hence increased feed requirements and uptake, and relatively longer calving intervals, implying compromised fertility. Furthermore, systematic upgrade of the local population based on the importation breeding strategy will have more potential in the cooler semi-temperate zones compared to the tropical regions. In all cases, this type of strategy must be combined with an improved level of management of animals across all seasons. The latter is especially important since this breeding strategy might be linked with increased feeding costs. Practical interventions including the mid-way house operational practice (African Dairy Genetic Gains, 2017) could complement and facilitate the implementation of these

breeding strategies. In Tanzania and other SSA, semen is currently being collected from randomly imported live bulls (not elite selected bulls) housed as a central authority like the National Artificial Insemination Centre (NAIC). These bulls are mainly of the Friesian, Ayrshire and Jersey breeds and sourced from Europe, USA, New Zealand, and neighbouring countries in Africa such as Kenya and South Africa. The collected semen is distributed to farmers in various regions of Tanzania by government and private extension officers. Semen selection from NAIC is often done by the inseminators. The current breeding policy is simply based on the use of this exotic semen to upgrade the indigenous cattle. As evidenced by results in the present study, such a strategy should consider bull selection based on the Overall Farmer Index, whereas random selection of exotic bulls would yield the least benefit.

In the present study, imported sires are expected to be genetically superior due to continual improvement in the country of origin. These sires would be also relevant to SSA since the selection will be based on the Overall Farmer Index. However, this may not be true since the elite bulls in the country of origin are not usually available for sale as live animals. Thus, there will be a limited selection of live bulls for sale that are not necessarily the best ones. A policy document for guiding the use of appropriate semen in different agro-ecological zones should be developed to embrace both the relative preference and predicted genetic gains for the individual breeding goal traits. A multilateral agreement between breeding companies in SSA and the country of origin of exotic sires should be developed to ensure the continuous supply of desired sire semen that suits smallholder farmers' breeding goals.

Because of limited resources and challenging production environments in smallholder farming systems, the importation breeding strategy is likely to be more expensive in the long-term than the other strategies due to costs associated with animal management (including stock replacement), health and fertility. This could have further implications when considering an adverse correlation between production and fitness traits, where the results of the sensitivity analysis carried out in the present study have revealed a reduction in the differences observed between strategies due to the lower fitness of highly productive exotic animals. Future studies should focus on a proper economic evaluation of all strategies. Careful co-ordination of semen importation will be important to ensure that semen is imported based on farmer trait preferences in different production environments. In these breeding programmes, organisations such as NAIC are expected to lead semen importation. In the long-term, governments in SSA will need to promote public–private partnership to ensure the availability of semen at affordable prices to smallholder farmers. Improvement of AI infrastructure will increase the rate of AI adoption.

Selection and utilisation of crossbred bulls to create a more productive and resilient synthetic breed within the smallholder system are also feasible. This breeding strategy was found to be more efficient when the level of exotic genes is maintained at around 50%. Under this strategy, a large number of F1 will be required at the beginning of the breeding programme. The next step will be to select and mate F1 heifers with F1 young bulls to produce F2. Under such a strategy, selected sires for each generation would be submitted to organisations like the NAIC for semen collection. This strategy might be more suitable for farmers in tropical areas characterised by low input production systems, where nearly equal emphasis is placed on fertility and milk production (Chawala et al., 2019). Therefore, a new synthetic breed might be suitable there because of improved CI and TEMP, and low BWT. Various studies have shown that synthetic breeds or crossbreds with 50% to 75% *B. taurus* genes are better suited in the challenging environments of the tropics compared to exotics (FAO, 2009; Galukande et al., 2013). Milk production and longevity are expected to increase with an increasing proportion of AI to create F1. However, the cost and benefit of using synthetic breeds compared to upgrades and/or indigenous need to be quantified before deciding on the best strategy for the tropical agro-ecological zone. Within each agro-ecological zone, central organisations in collaboration with multinational and local dairy breeding companies would be required to characterise the production systems to identify the most suitable genotype based on animal husbandry practices, feed availability, micro-climate and level of management.

The indigenous cattle improvement strategy based on the domestic selection of the best indigenous sires also has merit for the genetic conservation of local cattle breeds. Many SSA indigenous cattle are considered as endangered and their unique adaptive characteristics may be lost forever under upgrading and replacement strategies with exotic genotypes (Mwai et al., 2015). An estimated 32% of the indigenous cattle in Africa became extinct in the last century and another 22% are in danger of extinction (Rege, 1999). Although not competitive compared to the upgrade/importation and new synthetic breed strategies in terms of animal performance, selection and genetic improvement of indigenous cattle might be attractive to farmers in low input systems who wish to utilise and conserve local breeds.

Implementation of any of the three breeding strategies assessed in the present study will depend on a well-established national herd recording scheme (Chagunda et al., 2006; Opoola et al., 2019). In the first instance, a relatively simple recording scheme of the five preferred traits of the smallholder farmers should be established. The minimum amount of data to be recorded should include animal identity and pedigree, daily milk yield, date of calving,

periodic measurement of body weight, lactation number and temperament score. Practical methods for data recording such as use of girth-tapes for bodyweight measurement could be adopted. The genetic and phenotypic progress based on Reduced Farmer Index (LMY and CI) which are the two most important and possibly easiest to record trait was close enough to the Overall Farmer Index to warrant more direct implementation. The Reduced Farmer Index may provide a certain level of progress in the first instance, while the recording platform for the other traits is being developed.

The next priority should be in strengthening AI services, including the establishment of liquid nitrogen plants in the various agro-ecological zones, as was recommended by Chagunda et al. (1998) in Malawi. It is recommended that national genetic evaluation services be formed. These services will be responsible for genetically evaluating all recorded animals, identifying selection candidates, and assessing the genetic progress made over time. The national genetic evaluation service will work closely with the organisations such as NAIC, government, private extension officers and farmers participating in the programme. A solid communication strategy must be developed to enhance the dissemination of available information for the selected bulls and uptake by the end-users (farmers). This strategy should include periodic feedback to farmers on the performance of bulls and aim to specifically address farmer's needs. In this way, decisions on appropriate breeding strategies will be implemented based on a combination of what the providers of genetic material know and what farmers truly want and need.

In the present study, the selection of sires was based on estimated breeding values derived separately for each animal trait of interest. In reality, with an adequate amount of quality data in place, multi-trait analyses may be conducted leading to a higher accuracy of evaluation and faster genetic gain. This benefit would permeate all studied strategies.

Moreover, the use of genomic evaluation could solve some of the issues discussed above. Under SSA conditions, the development of specific SNP panels tailored to the needs of the breeding programme could be used to evaluate exotic animals prior to their importation and assess gene by environment interactions. Genomic selection has been shown to be a viable alternative in SSA cattle breeding (Kariuki et al., 2017) leading to genetic and economic gains. Nevertheless, as discussed above, reaping the benefits of any breeding strategy still depends on a well-established recording scheme for the key animal traits as well as good communication with farmers and active participation of the latter. Ongoing activities such as the African Dairy Genetic Gains project (2017) underpin the establishment of performance recording and the generation of genomic data for the development of genomic evaluation and selection programmes.

5 | CONCLUSIONS

Results of the present study demonstrated that upgrading indigenous cattle through systematic importation of appropriate exotic genetic material would lead to an overall higher genetic progress in the dairy population in SSA compared to developing a new synthetic breed or improving the indigenous breeds with domestic selection. Selection and importation of exotic sire semen should be based on the Overall Farmer Index of preferred traits identified by smallholder dairy farmers. Separate selection indexes could be derived based on animal trait preferences within different agro-ecological zones. This would optimise the improvement of dairy cattle performance in the prevailing smallholder farming systems in SSA. Increasing the proportion of cows participating in the genetic improvement programme would result in additional benefits. The results from this study provide an opportunity for breeding programme designers to choose the appropriate breeding strategy that fits a particular production environment.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The manuscript was based on simulation studies; no real data were used or generated.

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REFERENCES

- African Dairy Genetic Gains (ADGG) (2017). *More productive and profitable dairy cows*. International Livestock Research Institute. <https://africadgg.wordpress.com/2017/03/27/outcomes/>
- Agriculture and Horticulture Development Board (AHDB) (2018). *Profitable lifetime index – £PLI*. Agriculture and Horticulture Development Board (AHDB). <https://dairy.ahdb.org.uk/resources-library/technical-information/breeding-genetics/£pli-factsheet/#.XirHtmj7Tcu>
- Anderson, C. B. (2003). Lessons on healing from Naaman (2 Kings 5:1–27): An African-American Perspective. In I. A. Phiri, B. Haddad & M. Masenya (Eds.), *African Women, HIV/AIDS and faith communities* (pp. 23–43). Pietermaritzburg: Cluster Publications.
- Ayalew, W., Aliy, M., & Negussie, E. (2015). Milk production performance of Holstein Friesian dairy cows at Holetta Bull Dam Farm. *Ethiopia. Livestock Research for Rural Development*, 27(9), 173.
- Bazeley, K. (2016). Growing great heifers – Where it goes wrong and how to get it right. *Livestock*, 21(1), 91–98. <https://doi.org/10.12968/live.2016.21.2.91>
- Bunning, H., Simm, G., Wall, E., Chagunda, M. G. G., Banos, G., & Amer, P. (2018). Modelling crossbreeding in African cattle. *Proceedings of the 11th World Congress on Genetics Applied to Livestock Production, Auckland, New Zealand*, 11–497.
- Birhanu, T., Mohammed, T., Kedebe, K., & Tadesse, M. (2015). Estimation of crossbreeding parameters for milk production and reproduction traits in Holstein Friesian and Ethiopian Boran crosses. *Journal of Reproduction and Infertility*, 6, 63–69.
- Chagunda, M. G. G., Bruns, E. W., King, J. M., & Wollny, C. B. A. (2004). Evaluation of the breeding strategy for milk yield of Holstein Friesian cows on large-scale dairy farms in Malawi. *The Journal of Agricultural Science*, 142, 595–601. <https://doi.org/10.1017/S0021859604004666>
- Chagunda, M. G. G., Msiska, A. C. M., Wollny, C. B. A., Tchale, H., & Banda, J. W. (2006). An analysis of smallholder farmers' willingness to adopt dairy performance recording in Malawi. *Livestock Research for Rural Development*, 18(5), 66. <https://doi.org/10.1017/S0021859604004666>
- Chagunda, M. G. G., Mujibi, F. D. N., Dusingizimana, T., Kamana, O., Cheruiyot, E., & Mwai, O. A. (2018). Use of high density single nucleotide polymorphism (SNP) arrays to assess genetic diversity and population structure of dairy cattle in smallholder dairy systems: The case of Girinka Programme in Rwanda. *Frontiers in Genetics*, 9, 438. <https://doi.org/10.3389/fgene.2018.00438>
- Chagunda, M. G. G., Wollny, C. B. A., Bruns, E., & Kamwanja, L. A. (1998). Evaluation of the artificial insemination programme for small-scale dairy farms in Malawi. *Archiv Für Tierzucht/Archives of Animal Breeding*, 41(1/2), 45–51.
- Chawala, A. R., Banos, G., Peters, A., & Chagunda, M. G. G. (2019). Farmer-preferred traits in smallholder dairy farming systems in Tanzania. *Tropical Animal Health and Production*, 51(6), 1337–1344. <https://doi.org/10.1007/s11250-018-01796-9>
- Chawala, A. R., Mwai, A. O., Peters, A., Banos, G., & Chagunda, M. G. G. (2020). Towards a better understanding of breeding objectives and production performance of dairy cattle in sub-Saharan Africa: A systematic review and meta-analysis. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, 15(007), 1–15. <https://doi.org/10.1079/PAVSNNR202015007>
- Cunningham, E. P., & Syrtstad, O. (1987). *Crossbreeding of Bos indicus and Bos taurus for milk production in the tropics* (Vol. 68). Food and

- Agriculture Organization of the United Nations (ISBN 92-5-). <http://www.fao.org/docrep/009/t0095e/T0095E04.htm>
- Demeke, S., Naser, F. W. C., & Schoeman, S. J. (2004). Estimates of genetic parameters for Boran, Friesian and crosses of Friesian and Jersey with the Boran cattle in the tropical highlands of Ethiopia: reproduction traits. *Journal of Animal Breeding and Genetics*, 121(1), 57–65.
- Dickerson, G. E. (1973). Inbreeding and Heterosis in Animals. *Journal of Animal Science*, 1973(Symposium), 54–77. <https://doi.org/10.1093/ansci/1973.symposium.54>
- Do, C., Wasana, N., Cho, K., Choi, Y., Choi, T., Park, B., & Lee, D. (2013). The effect of age at first calving and calving interval on productive life and lifetime profit in Korean holsteins. *Asian-Australasian Journal of Animal Sciences*, 26(11), 1511–1517. <https://doi.org/10.5713/ajas.2013.13105>
- FAO (2009). *Selection and breeding of cattle in Asia: Strategies and criteria for improved breeding*. FAO, IAEA, VIENNA, 2009 IAEA-TECDOC-1620 ISBN 978-92-0-107209-2 ISSN 1011-4289. Animal Production and Health Section International Atomic Energy Agency Vienna International Centre P.O. Box 100 1400 Vienna, Austria. https://www-pub.iaea.org/MTCD/publications/PDF/te_1620_web.pdf
- FAOSTAT (2019). *Food and agriculture data*. Food and Agriculture Organization of the United Nations. FAOSTAT database. <http://www.fao.org/faostat/en/>
- Freetly, H. C., Kuehn, L. A., & Cundiff, L. V. (2011). Growth curves of crossbred cows sired by Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli bulls, and the fraction of mature body weight and height at puberty. *Journal of Animal Science*, 89, 2373–2379. <https://doi.org/10.2527/jas.2011-3847>
- Galukande, E. B., Mahadevan, P., & Black, J. G. (1962). Milk production in East African Zebu Cattle. *Animal Science*, 4(3), 329–336. <https://doi.org/10.1017/S0003356100040733>
- Galukande, E., Mulindwa, H., Wurzinger, M., Roschinsky, R., Mwai, A. O., & Sölkner, J. (2013). Cross-breeding cattle for milk production in the tropics: Achievements, challenges and opportunities. *Animal Genetic Resources: Food and Agriculture Organization of the United Nations*, 52, 111–125. <https://doi.org/10.1017/S2078633612000471>
- Haile-Mariam, M., & Kassa-Mersha, H. (1994). Genetic and environmental effects on age at first calving and calving interval of naturally bred Boran (zebu) cows in Ethiopia. *Animal Production*, 58(3), 329–334. <https://doi.org/10.1017/S000335610000725X>
- Haskell, M. J., Simm, G., & Turner, S. P. (2014). Genetic selection for temperament traits in dairy and beef cattle. *Frontiers in Genetics*, 5, 368. <https://doi.org/10.3389/fgene.2014.00368>
- Ilatsia, E. D., Migose, S. A., Muhuyi, W. B., & Kahi, A. K. (2011). Sahiwal cattle in semi-arid Kenya: Genetic aspects of growth and survival traits and their relationship to milk production and fertility. *Tropical Animal Health and Production*, 43, 1575–1582. <https://doi.org/10.1007/s11250-011-9845-x>
- Ilatsia, E. D., Muasya, T. K., Muhuyi, W. B., & Kahi, A. K. (2007). Genetic and phenotypic parameters and annual trends for milk production and fertility traits of the Sahiwal cattle in semi arid Kenya. *Tropical Animal Health and Production*, 39, 37–48. <https://doi.org/10.1007/s11250-006-4408-2>
- Interbull (2019). *National genetic evaluations*. Interbull. <https://interbull.org/ib/geforms/>
- Kariuki, C. M., Brascamp, E. W., Komen, H., Kahi, A. K., & van Arendonk, J. A. M. (2017). Economic evaluation of progeny-testing and genomic selection schemes for small-sized nucleus dairy cattle breeding programs in developing countries. *Journal of Dairy Science*, 100(3), 2258–2268. <https://doi.org/10.3168/jds.2016-11816>
- Kern, E. L., Cobuci, A., Cobuci, J. A., Costa, C. N., Neto, J. B., Campos, G. S., & McManus, C. M. (2014). Genetic parameters for longevity measures in Brazilian Holstein cattle using linear and threshold models. *Archiv Tierzucht*, 57(33), 1–12. <https://doi.org/10.7482/0003-9438-57-033>
- Lin, B. Z., Sasazaki, S., & Mannen, H. (2010). Genetic diversity and structure in *Bos taurus* and *Bos indicus* populations analyzed by SNP markers. *Animal Science Journal*, 81(3), 281–289. <https://doi.org/10.1111/j.1740-0929.2010.00744.x>
- Loftus, R. T., Machugh, D. E., Bradley, D. G., Sharp, P. M., & Cunningham, P. (1994). Evidence for two independent domestications of cattle. *Proceedings of the National Academy of Sciences of the United States of America*, 91(7), 2757–2761. <https://doi.org/10.1073/pnas.91.7.2757>
- Mahadevan, P., Galukande, E. B., & Black, J. G. (1962). A genetic study of the Sahiwal grading-up scheme in Kenya. *Animal Science*, 4(3), 337–342. <https://doi.org/10.1017/S0003356100040745>
- Marshall, K., Gibson, J. P., Mwai, O., Mwacharo, J. M., Haile, A., Getachew, T., Mrode, R., & Kemp, S. J. (2019). Livestock genomics for developing countries – African examples in practice. *Frontiers in Genetics*, 10, 297. <https://doi.org/10.3389/fgene.2019.00297>
- McDowell, R. E. (1985). Crossbreeding in tropical areas with emphasis on milk, health, and fitness. *Journal of Dairy Science*, 68(9), 2418–2435. [https://doi.org/10.3168/jds.S0022-0302\(85\)81118-8](https://doi.org/10.3168/jds.S0022-0302(85)81118-8)
- Michael, S., Mbwambo, N., Mruttu, H., Dotto, M. M., Ndomba, C., Da Silva, M., & Gebru, G. (2018). *Tanzania livestock master plan*. International Livestock Research Institute (ILRI). https://cgspac.ce.cgiar.org/bitstream/handle/10568/92405/livestockMasterPlan_Tanzania.pdf?sequence=1
- Moran, J. (Ed.) (2012). Young stock management. In *Managing high grade dairy cows in the tropics* (pp. 47–50). CSIRO Publishing. ISBN: 978-0-643-10790-8. <https://doi.org/10.1071/9780643107892>
- Mujibi, F. D. N., Rao, J., Agaba, M., Nyambo, D., Cheruiyot, E. K., Kihara, A., Zhang, Y. I., & Mrode, R. (2019). Performance evaluation of highly admixed Tanzanian smallholder dairy cattle using SNP derived kinship matrix. *Frontiers in Genetics*, 10, 375. <https://doi.org/10.3389/fgene.2019.00375>
- Mungube, E. O., Njarui, D. M. G., Maichomo, M. W., Olum, M. O., Ndirangu, P. N., Kabirizi, J., & Mwangi, G. (2019). Reproductive performance indicators of dairy cattle in selected small-scale dairy farms in semi-arid Eastern Kenya. *Livestock Research for Rural Development*, 31, 88.
- Musingi, B. M., Muasya, T. K., & Kahi, A. K. (2018). Genetic parameters for measures of longevity in Kenyan Sahiwal cattle. *Livestock Research for Rural Development*, 30, 96.
- Mwai, O., Hanotte, O., Kwon, Y. J., & Cho, S. (2015). Invited review – African indigenous cattle: Unique genetic resources in a rapidly changing world. *Asian-Australasian Journal of Animal Sciences*, 28(7), 911–921. <https://doi.org/10.5713/ajas.15.0002R>
- Mwanga, G., Mujibi, F. D. N., Yohah, Z. O., & Chagunda, M. G. G. (2019). Multi-country investigation of factors influencing breeding decisions by smallholder dairy farmers in sub-Saharan Africa. *Tropical Animal Health and Production*, 51, 395–409. <https://doi.org/10.1007/s11250-018-1703-7>
- National Bureau of Statistics (NBS) (2015). *Tanzania National Bureau of Statistics: Annual agricultural sample survey report (Crops and Livestock Report) – 2014/15*. National Bureau of Statistics (NBS). <https://www.nbs.go.tz/index.php/en/census-surveys/agricultur>

- e-statistics/56-2014-15-annual-agricultural-sample-survey-crops-and-livestock-report
- Neja, W., Sawa, A., Jankowska, M., Bogucki, M., & Krężel-Czopek, S. (2015). Effect of the temperament of dairy cows on lifetime production efficiency. *Archives Animal Breeding*, 58, 193–197. <https://doi.org/10.5194/aab-58-193-2015>
- Ojango, J. M., & Pollott, G. E. (2001). Genetics of milk yield and fertility traits in Holstein-Friesian cattle on large-scale Kenyan farms. *Journal of Animal Science*, 79(7), 1742–1750. <https://doi.org/10.2527/2001.7971742x>
- Oldenbroek, K., & van der Waaij, L. (2015). *Textbook Animal Breeding and Genetics for BSc students: Chapter 8.11: Accuracy of estimated breeding values*. The Netherlands and Animal Breeding and Genomics Centre website. <https://wiki.groenkennisnet.nl/display/TAB/Textbook+Animal+Breeding+and+Genetics>
- Olori, V. E., Meuwissen, T. H. E., & Veerkamp, R. F. (2002). Calving interval and survival breeding values as measure of cow fertility in a pasture-based production system with seasonal calving. *Journal of Dairy Science*, 85(3), 689–696. [https://doi.org/10.3168/jds.S0022-0302\(02\)74125-8](https://doi.org/10.3168/jds.S0022-0302(02)74125-8)
- Opoola, O. (2018). *Across country dairy breeding strategies in Sub-Saharan Africa*. PhD Thesis, The University of Edinburgh.
- Opoola, O., Mrode, R., Banos, G., Ojango, J., Banga, C., Simm, G., & Chagunda, M. G. G. (2019). Current situations of animal data recording, dairy improvement infrastructure, human capacity and strategic issues affecting dairy production in sub-Saharan Africa. *Tropical Animal Health and Production*, 51, 1699–1705. <https://doi.org/10.1007/s11250-019-01871-9>
- Pérez-Cabal, M. A., & Alenda, R. (2003). Lifetime profit as an individual trait and prediction of its breeding values in Spanish Holstein cows. *Journal of Dairy Science*, 86(12), 4115–4122. [https://doi.org/10.3168/jds.S0022-0302\(03\)74025-9](https://doi.org/10.3168/jds.S0022-0302(03)74025-9)
- Pritchard, T., Coffey, M., Mrode, R., & Wall, E. (2013). Genetic parameters for production, health, fertility and longevity traits in dairy cows. *Animal*, 7(1), 34–46. <https://doi.org/10.1017/S1751731112001401>
- Rege, J. E. O. (1999). The state of African cattle genetic resources I. Classification framework and identification of threatened and extinct breeds. In J. Hodges, J. Boyazoglu, J. E. O. Rege, J. S. F. Barker & G. L. H. Alderson (Eds.), *Animal genetic resources information* (25th ed., p. 21). Cambridge University Press.
- Rutledge, J. J. (2001). Greek temples, tropical kine and recombination load. *Livestock Production Science*, 68(2–3), 171–179. [https://doi.org/10.1016/S0301-6226\(00\)00245-1](https://doi.org/10.1016/S0301-6226(00)00245-1)
- Salami, A., Kamara, A. B., & Brixiova, Z. (2010). *Smallholder agriculture in East Africa: Trends, constraints and opportunities*. Working Paper No. 105. African Development Bank, Tunis, Tunisia.
- Shapiro, B. I., Gebru, G., Desta, S., Negassa, A., & Nigussie, K. (2017). *Rwanda livestock master plan*. ILRI Project Report. International Livestock Research Institute (ILRI).
- Shapiro, B. I., Gebru, G., Desta, S., Negassa, A., Nigussie, K., Aboset, G., & Mechal, H. (2015). *Ethiopia livestock master plan*. ILRI Project Report. International Livestock Research Institute (ILRI).
- Sharma, B. S., Prabhakaran, V. T., & Pirchner, F. (2000). Gene action and heterosis in lifetime traits of Friesian × Sahiwal crosses. *Journal of Animal Breeding and Genetics*, 117, 319–330.
- Singh, C. V. (2015). Cross-breeding in cattle for milk production: Achievements, challenges and opportunities in India – A review. *Advances in Dairy Research*, 4(3), 1–14.
- Somda, J., Kamuanga, M., & Tollens, E. (2005). Characteristics and economic viability of milk production in the smallholder farming systems in The Gambia. *Agricultural Systems*, 85(1), 42–58. <https://doi.org/10.1016/j.agsy.2004.07.011>
- Syrstad, O. (1985). Heterosis in *Bos taurus* × *Bos indicus* crosses. *Livestock Production Science*, 12(4), 299–307. [https://doi.org/10.1016/0301-6226\(85\)90130-7](https://doi.org/10.1016/0301-6226(85)90130-7)
- United Republic of Tanzania (URT) (2019). *National Livestock Research Agenda 2020–2015* (pp. 1–13). The United Republic of Tanzania. Ministry of Livestock and Fisheries Development.
- Vaccaro, L., Pérez, A., & Vaccaro, R. (1999). Productive performance of F1 compared with other 50% European-zebu crossbred cows for dual purpose systems in the Venezuelan tropics. *Livestock Research for Rural Development*, 11, 3.
- Wall, E., Brotherstone, S., Kearney, J., Woolliams, J., & Coffey, M. (2005). Impact of nonadditive genetic effects in the estimation of breeding values for fertility and correlated traits. *Journal of Dairy Science*, 88, 376–385. [https://doi.org/10.3168/jds.S0022-0302\(05\)72697-7](https://doi.org/10.3168/jds.S0022-0302(05)72697-7)
- Wasike, C. B., Indetie, D., Ojango, J. M. K., & Kahi, A. K. (2009). Direct and maternal (co)variance components and genetic parameters for growth and reproductive traits in the Boran cattle in Kenya. *Tropical Animal Health and Production*, 41(5), 741–748. <https://doi.org/10.1007/s11250-008-9246-y>

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APPENDIX 1

Breeding goal traits and selection indexes with relative trait emphasis on smallholder farmer preferred traits.

Farmer preferences	Breeding goal traits (abbreviation)	Index for selection and emphasis (weights) placed on each trait		Trait description and desired direction of change in a breeding programme in Sub-Saharan Africa
		OFI (β)	RFI (β)	
High milk yield	Lactation milk yield (LMY)	1.43	1.43	Kilograms of milk yield in a 305-day lactation; high values are desirable
Good fertility	Calving interval (CI)	−0.85	−0.85	Number of days between two consecutive calvings; low numbers are desirable
Easy temperament	Temperament (TEMP)	0.76		Temperament score measured on a 1–9 scale; high scores are desirable
Low feed intake	Mature live weight (BWT)	−0.56		Average mature live weight (kg); aim is to avoid increasing
Disease resistance	Longevity (LF)	0.48		Lifespan score reflecting the number of lactations completed; high values are desirable

Note: OFI = Relative weights for an Overall Farmer Index (β); RFI = Relative weights for a Reduced Farmer Index (β); from Chawala et al. (2019).

APPENDIX 2

Breeding goal traits and selection indexes with relative trait emphasis in the exporting country (exotic index).

Breeding goal traits	Index for selection and emphasis (weights) placed on each trait (£)	Trait description and desired direction of change for exotic index
Lactation milk yield (LMY)	−0.02	Kilograms of milk yield in a 305-day lactation; high values are desirable
Calving interval (CI)	−0.35	Number of days between two consecutive calvings; low numbers are desirable
Temperament (TEMP)	0	Temperament score measured on a 1–9 scale; high scores are desirable
Mature live-weight (BWT)	0	Average mature live weight (kg); aim is to avoid increasing
Longevity (LF)	25.4	Lifespan score reflecting the number of lactations completed; high values are desirable
Fat yield (Fat)	0.08	Kilograms of milk fat yield in a 305-day lactation; high values are desirable
Protein yield (Protein)	1.71	Kilograms of milk protein yield in a 305-day lactation; high values are desirable
Somatic cell count (SCC)	−0.19	Log-transformed milk somatic cell count as an indicator of mastitis; low values are desirable
Feet and legs (Feet)	1.13	Composite of linear type traits related to legs and feet measured on a scale of 50–90; high values are desirable
Mammary systems (Udder)	1.88	Composite of linear type traits related to udder measured on a scale of 50–90; high values are desirable
Non-return at 56 days (NR56)	2.16	Non-return to service after 56 days; 1 = return to service; 2 = no return to service (i.e. presumed to have conceived); high values are desirable

Note: From: AHDB (2018), Interbull (2019), Pritchard et al. (2013), Wall et al. (2005).

APPENDIX 3

Breeding strategies and selection scenarios of dairy cattle in smallholder dairy farms.

Breeding strategy	Selection scenario
Strategy A: Genetic improvement through continuous importation of selected exotic sires leading to a gradual upgrade of the indigenous population	Scenario A1: Selection of exotic sires based on the Overall Farmer Index (Appendix 1)
	Scenario A2: Selection of exotic sires based on the Reduced Farmer Index (Appendix 1)
	Scenario A3: Selection of exotic sires based on the Exotic Index (Appendix 2)
	Scenario A4: Random Selection of exotic sires
Strategy B: Creation of new synthetic breed through importation of selected exotic sires in first generation and subsequent selection of crossbred sires	Scenario B5: Selection of sires based on the Overall Farmer Index (Appendix 1)
Strategy C: Genetic improvement of indigenous population through genetic selection of local sires	Scenario C6: Selection of indigenous sires based on the Overall Farmer Index (Appendix 1)

APPENDIX 4

Estimates of genetic variance and heritability (in parenthesis) of farmer preferred traits in the exotic and sub-Saharan African (SSA) populations.

Trait (units of measurement)	Exotic animal performance in country of origin	Exotic animal performance in SSA	Indigenous animal performance in SSA
LMY (kg)	557,440 (0.55) ^a	360,274 (0.29) ^d	353,422 (0.21) ^g
CI (days)	137.72 (0.02) ^a	272.00 (0.05) ^d	246.28 (0.03) ^h
TEMP (1–9 scale)	0.10 (0.10) ^b	0.10 (0.10) ^e	0.10 (0.10) ^e
BWT (kg)	501.00 (0.32) ^c	442.68 (0.32) ^e	211.00 (0.20) ⁱ
LF (number of lactations)	0.43 (0.06) ^a	0.15 (0.09) ^f	0.06 (0.04) ^j

Note: LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations).^a Source: Pritchard et al. (2013).^b Interbull (2019).^c Pérez-Cabal and Alenda (2003).^d Ayalew et al. (2015), Ojango and Pollott (2001), Opoola (2018).^e Parameter scaled to African environment.^f Kern et al. (2014).^g Ilatsia et al. (2007).^h Haile-Mariam and Kassa-Mersha (1994), Ilatsia et al. (2007), Wasike et al. (2009).ⁱ Ilatsia et al. (2011).^j Musingi et al. (2018).

APPENDIX 5

Genetic correlation estimates among simulated traits (above the diagonal) and between the exotic and sub-Saharan African population for the same trait (diagonal).

Traits	LMY ^a	Fat ^b	Protein ^b	LF ^a	SCC ^b	Feet ^b	Udder ^b	NR56 ^b	CI ^a	BWT ^a	TEMP ^a
LMY	0.81	0.61	0.85	0.00	0.18	−0.07	0.00	−0.42	0.47	0.23	0.44
Fat		0.81	0.69	−0.13	0.19	−0.04	0.00	−0.30	0.46	0.26	0.24
Protein			0.81	−0.14	0.22	−0.07	0.00	−0.43	0.45	0.25	0.25
LF				0.9	−0.07	0.64	0.26	0.08	−0.50	−0.10	0.18
SCC					0.92	0.04	−0.21	−0.12	0.13	0.23	−0.41
Feet						0.93	0.21	−0.16	−0.01	0.03	0.21
Udder							0.98	−0.10	0.14	−0.24	0.20
NR56								0.80	−0.35	−0.19	0.11
CI									0.87	0.01	0.05

(Continues)

APPENDIX 5 (Continued)

Traits	LMY ^a	Fat ^b	Protein ^b	LF ^a	SCC ^b	Feet ^b	Udder ^b	NR56 ^b	CI ^a	BWT ^a	TEMP ^a
BWT										0.94	-0.02
TEMP											0.85

Note: LMY = milk yield (kg) in a 305-day lactation; Fat = Fat yield (kg) in a 305-day lactation, Protein = Protein yield (kg) in a 305-day lactation, LF = longevity (number of lactations), CI = calving interval (days), BWT = mature live body weight (kg), SCS = Log-transformed somatic cell count score, Feet = Composite of linear type traits related to legs and feet (50–90 scale), Udder = Composite of linear type traits related to udder (50–90 scale), NR56 = Non-return to service (1=returned to service, 2 = Conceived and did not return to service), TEMP = temperament score (1–9 scale).^a Chawala et al. (2019).^b Interbull (2019).

APPENDIX 6

Phenotypic average describing performance of exotic and indigenous cattle for farmer preferred traits.

Trait	Exotic animal performance in country of origin	Exotic animal performance in SSA	Indigenous animal performance in SSA
LMY (kg)	8,065 ^a	4,050 ^d	1,363 ^g
CI (days)	402 ^a	462 ^d	450 ^h
TEMP (1–9 scale)	5.5 ^b	4.7 ^e	4.7 ^e
BWT (kg)	648 ^c	557 ^e	337 ⁱ
LF (number of lactations)	4.7 ^a	2.68 ^f	2.7 ^j

Note: SSA = sub-Saharan Africa; LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations).^a Source: Pritchard et al. (2013).^b Interbull (2019).^c Pérez-Cabal and Alenda (2003).^d Ayalew et al. (2015), Ojango and Pollott (2001), Opoola (2018).^e Parameter scaled to African environment.^f Kern et al. (2014).^g Ilatsia et al. (2007).^h Haile-Mariam and Kassa-Mersha (1994), Ilatsia et al. (2007), Wasike et al. (2009).ⁱ Ilatsia et al. (2011).^j Musingi et al. (2018).

APPENDIX 7

Estimates of maximum heterosis and recombination loss for breeding goal traits in smallholder dairy production systems.

Trait	Maximum heterosis in F1 (%)	Parental Mean (F1) ^a	Maximum heterosis in F1
LMY (kg)	35%	2,706.50	947.28
CI (days)	12%	456.00	-54.72
BWT (kg)	12%	447.00	53.64
LF (No. of lactations)	35%	2.69	0.94
TEMP (1–9 scale)	0.0%	4.70	0

^a Parental mean is calculated from phenotypic performance of exotic and indigenous populations in sub-Saharan Africa shown in Appendix 6.

Source: Bunning et al. (2018), Birhanu et al. (2015), Demeke et al. (2004), Sharma et al. (2000).

APPENDIX 8

Average inbreeding coefficient per generation, selection scenario and percentage AI scheme. Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

APPENDIX 9

Predicted genetic trends for individual animal traits in smallholder dairy systems at 50% (Y) and 30% (Z) AI schemes: LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

APPENDIX 10

Average predicted rate of genetic gain per generation from generation 0 to 5. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

AI-scheme	Scenario	LMY (kg)	CI (days)	BWT (kg)	LF (No. lactations)	Temp (1–9 scale)
100%	A1	753.6	3.10	42.13	0.11	0.11
	A2	770.0	3.70	44.20	0.07	0.08
	A3	773.9	3.65	43.65	0.07	0.07
	A4	668.3	3.09	42.73	0.06	0.05
	B5	439.9	1.69	14.91	0.08	0.13
	C6	217.0	0.65	−1.10	0.04	0.10
50%	A1	594.6	2.44	35.10	0.08	0.08
	A2	609.4	2.90	36.89	0.05	0.06
	A3	609.1	2.86	36.16	0.05	0.05
	A4	521.4	2.41	35.72	0.03	0.03
	B5	255.9	0.48	11.71	0.05	0.07
	C6	115.6	0.17	−0.46	0.02	0.05
30%	A1	427.3	1.70	25.75	0.05	0.06
	A2	438.7	2.08	27.05	0.03	0.04
	A3	443.6	2.13	26.81	0.03	0.03
	A4	373.6	1.69	26.12	0.02	0.02
	B5	155.3	0.30	6.98	0.02	0.04
	C6	69.6	0.10	−0.35	0.01	0.03

APPENDIX 11

Average predicted rate of genetic gain per generation from generation 6 to 15. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the

Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

AI-scheme	Scenario	LMY (kg)	CI (days)	BWT (kg)	LF (No. lactations)	Temp (1–9 scale)
100%	A1	276.3	1.15	2.01	0.09	0.07
	A2	278.7	1.22	2.12	0.09	0.07
	A3	281.6	1.38	2.60	0.09	0.06
	A4	277.7	1.20	2.20	0.09	0.07
	B5	249.8	0.76	−1.21	0.07	0.12
	C6	246.0	0.52	−0.99	0.05	0.11
50%	A1	311.1	1.41	5.64	0.09	0.07
	A2	313.8	1.47	5.80	0.08	0.07
	A3	316.6	1.58	6.17	0.08	0.06
	A4	303.7	1.35	5.67	0.08	0.07
	B5	138.8	0.37	−0.70	0.03	0.07
	C6	138.1	0.24	−0.69	0.03	0.06
30%	A1	317.7	1.35	8.64	0.08	0.07
	A2	321.1	1.45	9.00	0.07	0.06
	A3	324.4	1.61	9.18	0.07	0.05
	A4	304.3	1.36	8.79	0.07	0.06
	B5	84.2	0.13	−0.50	0.02	0.04
	C6	85.0	0.12	−0.43	0.02	0.04

APPENDIX 12

Predicted genetic trends for individual animal traits in country of origin of exotic sires after 15 generation of selection based on the Exotic Index: LMY = milk yield (kg) in a 305-day lactation; Fat = Fat yield (kg) in a 305-day lactation, Protein = Protein yield (kg) in a 305-day lactation, LF = longevity (number of lactations), CI = calving interval (days), BWT = mature live body weight (kg), SCS = Log-transformed somatic cell count score, Feet = Composite of linear type traits related to legs and feet (50–90 scale), Udder = Composite of linear type traits related to udder (50–90 scale), NR56 = Non-return to service (1=returned to service, 2=conceived and did not return to service), TEMP = temperament score (1–9 scale).

APPENDIX 13

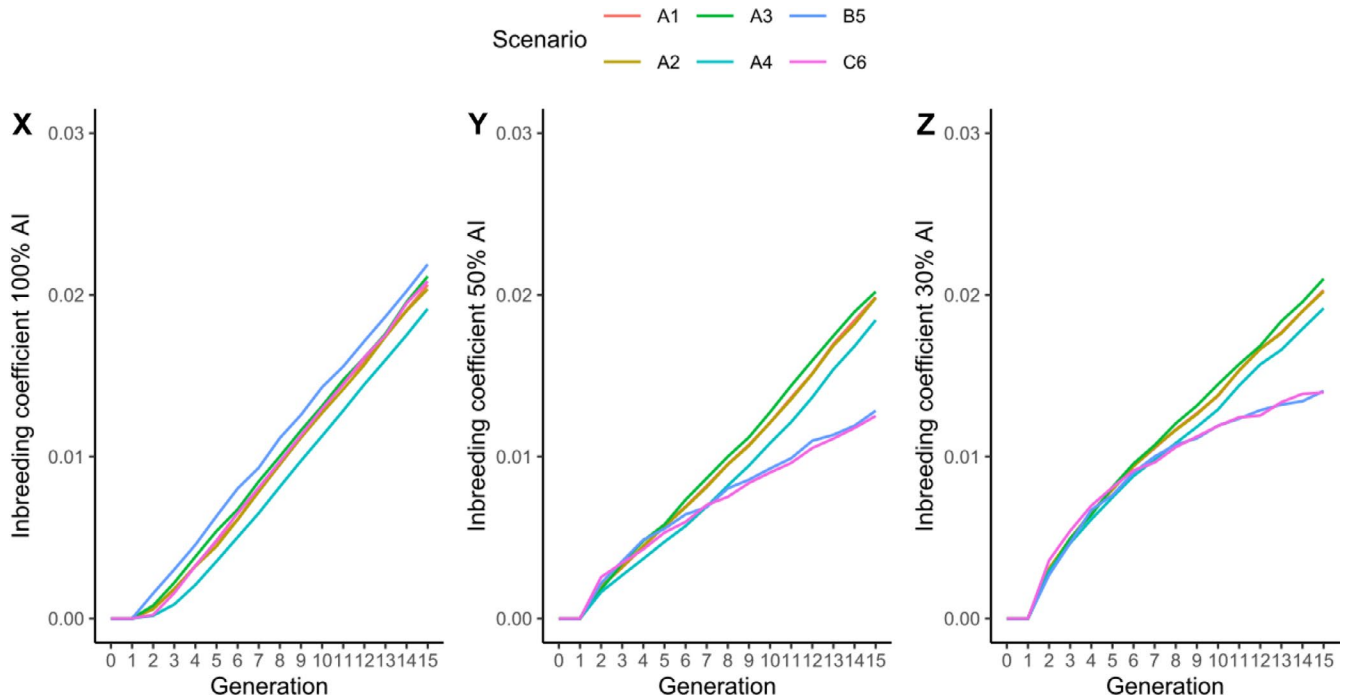
Predicted phenotypic trends for individual animal traits in smallholder dairy systems at 50% (Y) and 30% (Z) AI schemes. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

APPENDIX 14

Predicted genetic trends in the Overall Farmer Index in the tropical agro-ecological zone at 100% (X), 50% (Y) and 30% (Z) AI schemes. Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

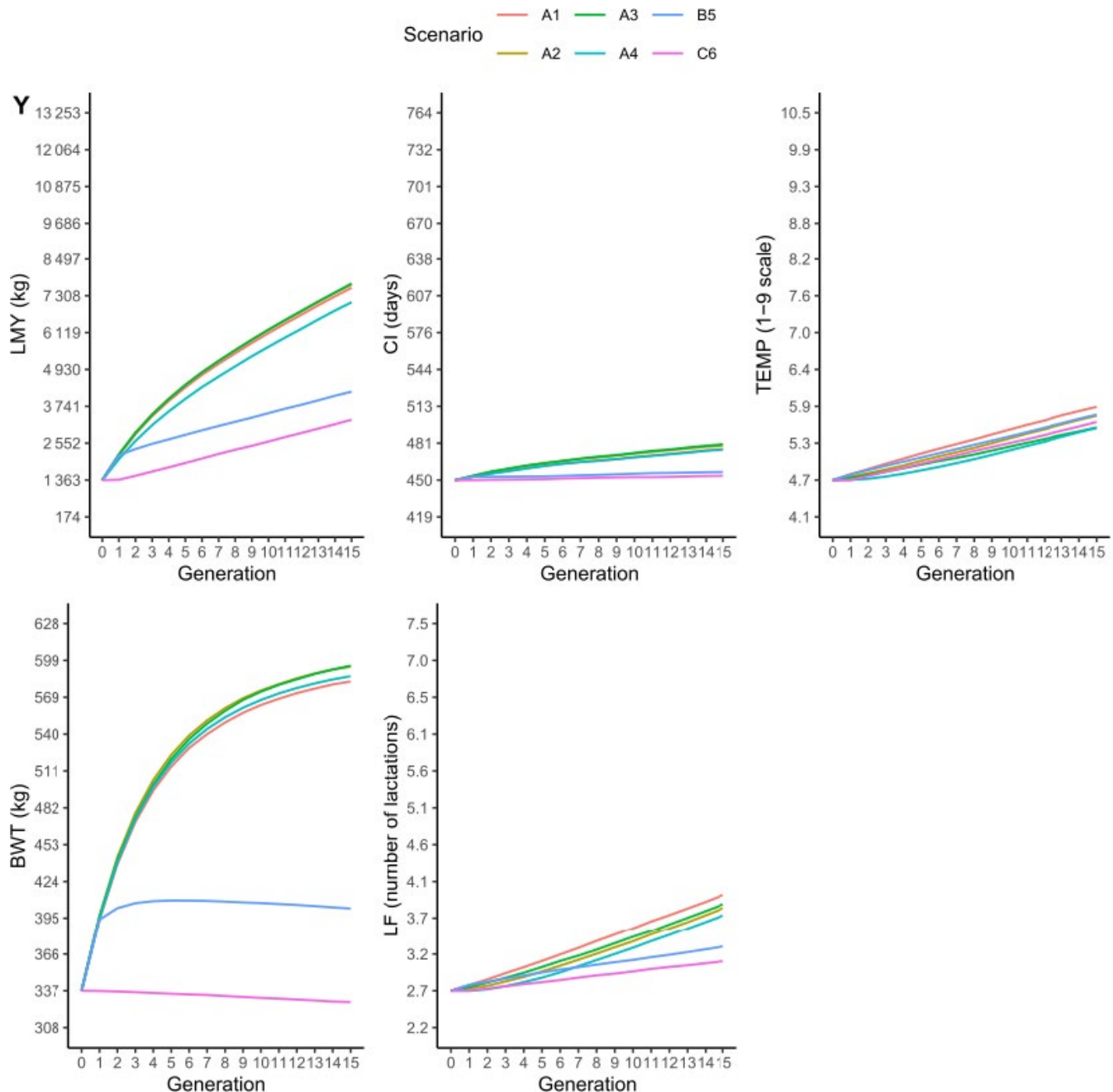
APPENDIX 15

Predicted genetic trends in the Overall Farmer Index in the semi-temperate agro-ecological zone at 100% (X), 50% (Y) and 30% (Z) AI schemes. Scenarios A1–A4 pertain imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).



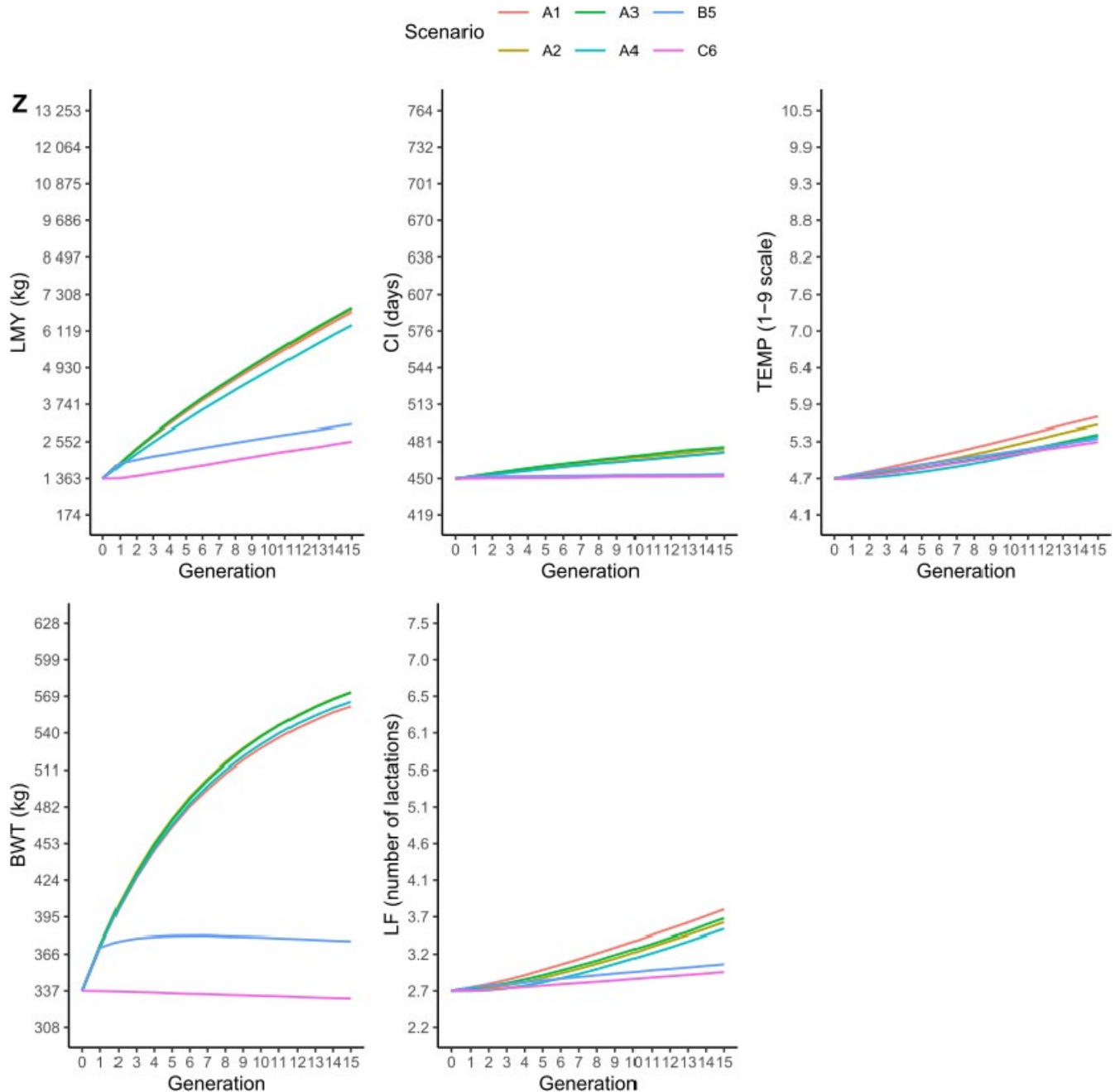
APPENDIX 16

Predicted genetic trends for individual animal traits in the tropical agro-ecological zone at 100% (X), 50% (Y) and 30% (Z) AI schemes. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).



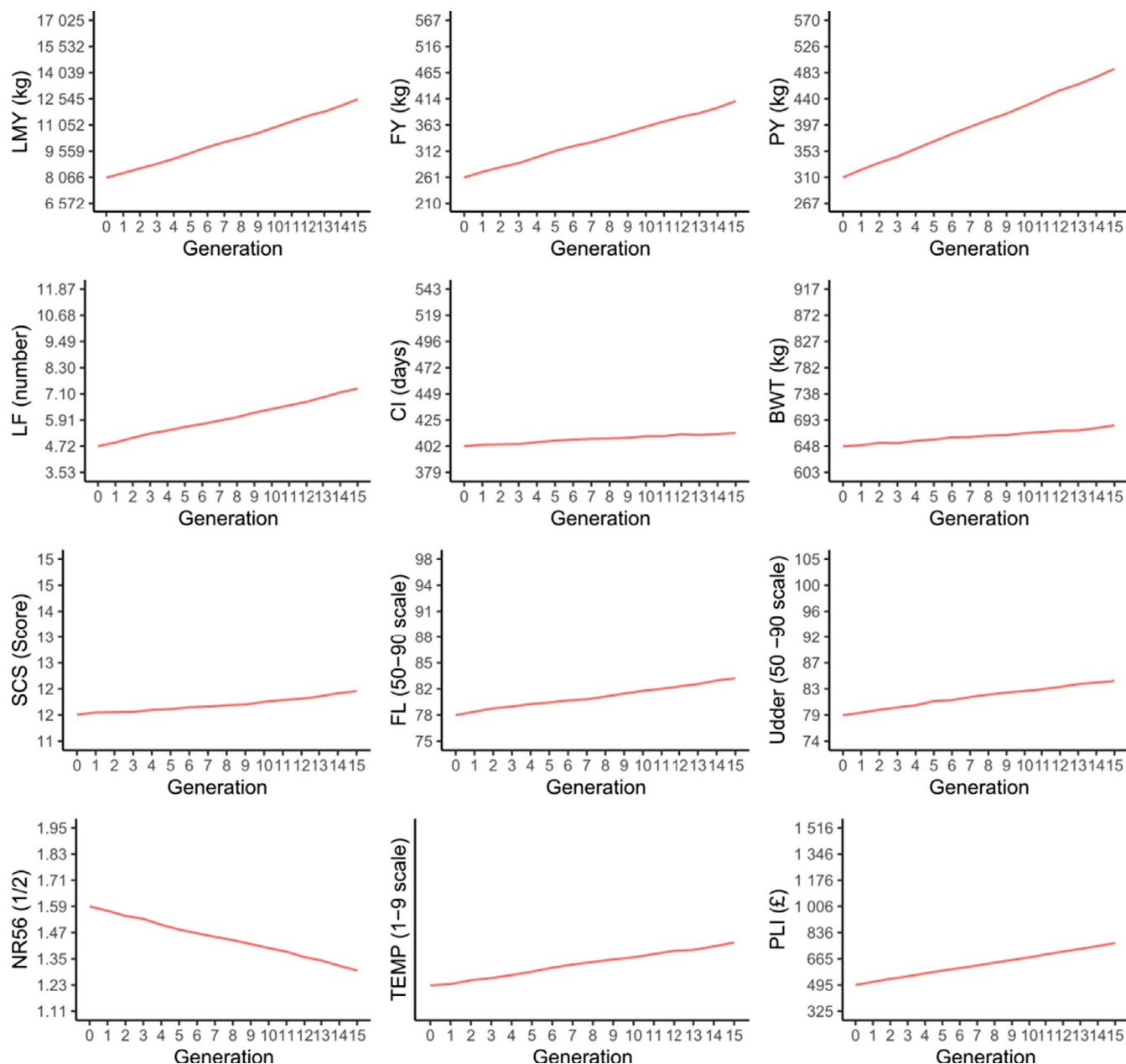
APPENDIX 17

Predicted genetic trends for individual animal traits in the semi-temperate agro-ecological zone at 100% (X), 50% (Y) and 30% (Z) AI schemes. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).



APPENDIX 18

Relative differences (%) in predicted genetic gain in individual animal traits and the Overall Farmer Index after 15 generations of selection in semi-temperate and tropical zone between Scenarios A1 (Importation strategy), B5 (Synthetic breed strategy) and C6 (Indigenous breed improvement strategy). LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations).



Zone	AI-Scheme	Scenario comparison	Difference (%)					Overall Farmer Index
			LMY	CI	BWT	LF	TEMP	
Semi-temperate	100%	A1 versus B5	13.95%	−0.34%	24.89%	12.60%	−7.62%	14.66%
	50%	A1 versus B5	39.71%	2.86%	29.28%	18.39%	2.81%	47.02%
	30%	A1 versus B5	50.44%	3.35%	31.83%	19.40%	6.54%	61.99
	100%	A1 versus C6	33.60%	1.69%	44.09%	20.19%	−4.50%	37.07%
	50%	A1 versus C6	52.61%	3.71%	43.01%	22.38%	4.37%	61.74%
	30%	A1 versus C6	59.40%	3.86%	40.66%	21.66%	7.07%	72.47%
Tropical	100%	A1 versus B5	30.95%	6.34%	27.02%	4.61%	−10.36%	28.72%
	50%	A1 versus B5	50.77%	5.88%	31.64%	16.04%	2.05%	57.11%
	30%	A1 versus B5	52.97%	3.19%	32.85%	19.89%	6.20%	63.86%
	100%	A1 versus C6	39.44%	3.22%	45.27%	19.03%	−5.20%	39.78%
	50%	A1 versus C6	61.86%	6.14%	43.89%	21.43%	3.75%	69.47%
	30%	A1 versus C6	61.35%	3.55%	40.93%	22.54%	7.03%	73.27%

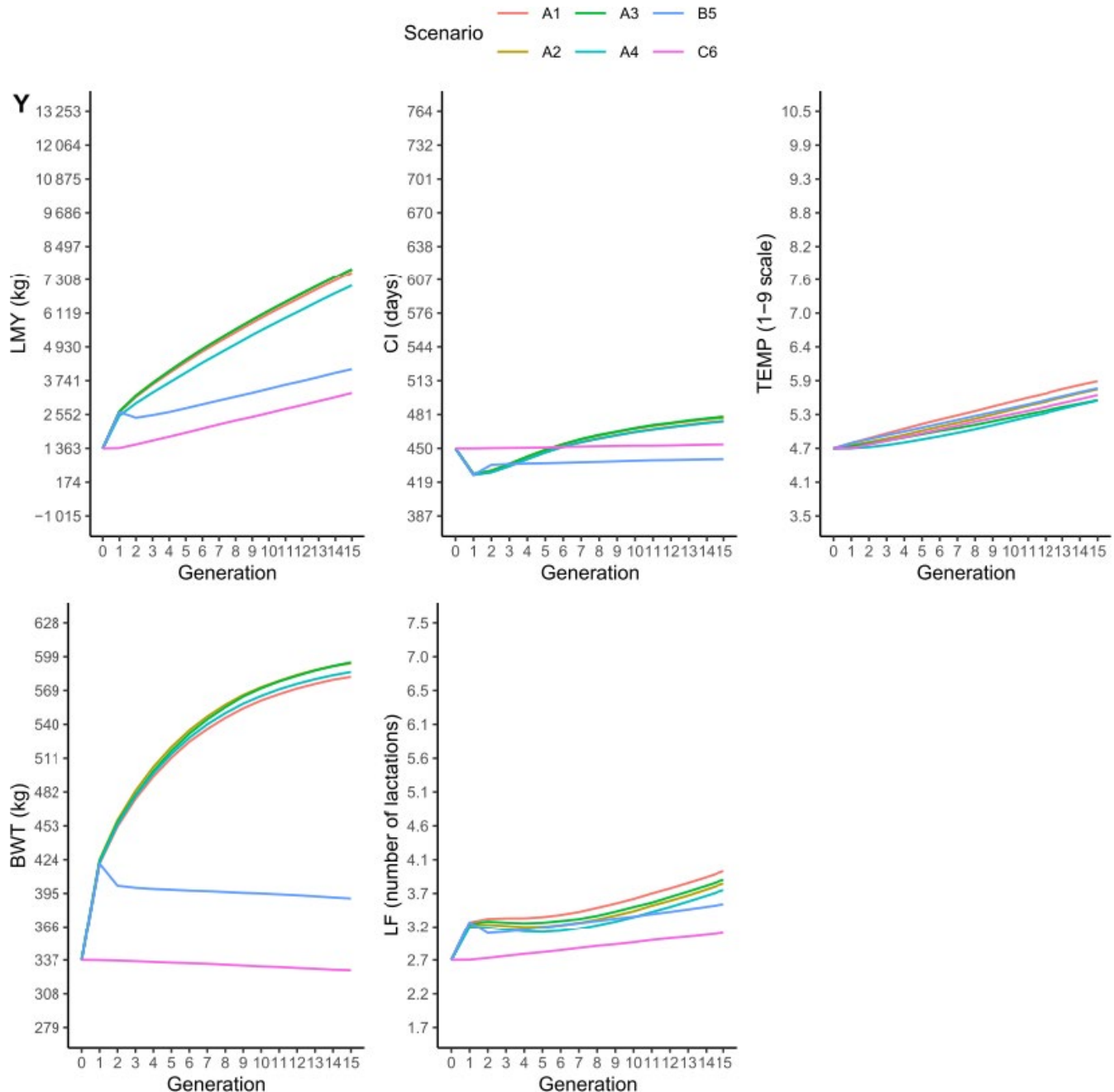
APPENDIX 19

Relative differences (%) in predicted genetic gain in individual animal traits and the Overall Farer Index after 15 generations of selection across and within agro-ecological zone between Scenarios A1 (Importation strategy), B5 (Synthetic breed strategy) and C6 (Indigenous breed improvement strategy); performance of exotics in sub-Saharan Africa was assumed to be reduced by 25% compared to the base simulation design. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations).

Zone	AI-Scheme	Scenario comparison	Difference (%)					Overall Farmer Index
			LMY	CI	BWT	LF	TEMP	
Across zones	100%	A1 versus B5	16.22%	11.57%	29.23%	0.79%	−24.35%	10.70%
	50%	A1 versus B5	43.63%	18.87%	40.91%	7.04%	−16.33%	47.59%
	30%	A1 versus B5	51.61%	19.21%	41.63%	6.84%	−13.13%	61.11%
	100%	A1 versus C6	32.02%	22.89%	51.73%	1.85%	−31.60%	24.74%
	50%	A1 versus C6	49.59%	23.24%	50.20%	6.28%	−20.26%	52.35%
	30%	A1 versus C6	56.12%	21.88%	47.68%	6.13%	−15.30%	65.18%
Semi-temperate	100%	A1 versus B5	9.34%	9.27%	27.98%	5.61%	−21.71%	5.93%
	50%	A1 versus B5	39.07%	17.12%	38.85%	7.67%	−14.98%	44.62%
	30%	A1 versus B5	48.29%	18.28%	40.48%	7.19%	−12.01%	58.91%
	100%	A1 versus C6	23.85%	20.49%	50.72%	4.52%	−29.95%	19.86%
	50%	A1 versus C6	45.84%	22.21%	49.94%	6.22%	−19.26%	50.97%
	30%	A1 versus C6	53.56%	21.23%	47.53%	5.42%	−14.39%	64.35%
Tropical	100%	A1 versus B5	28.18%	14.94%	29.71%	−4.14%	−25.47%	19.75%
	50%	A1 versus B5	50.67%	20.77%	42.62%	6.62%	−17.27%	52.09%
	30%	A1 versus B5	55.86%	20.03%	42.40%	6.88%	−13.08%	63.51%
	100%	A1 versus C6	42.03%	25.57%	52.11%	−0.68%	−33.40%	28.39%
	50%	A1 versus C6	55.93%	24.50%	50.45%	5.71%	−20.65%	54.97%
	30%	A1 versus C6	59.85%	22.53%	47.72%	5.83%	−15.43%	65.84%

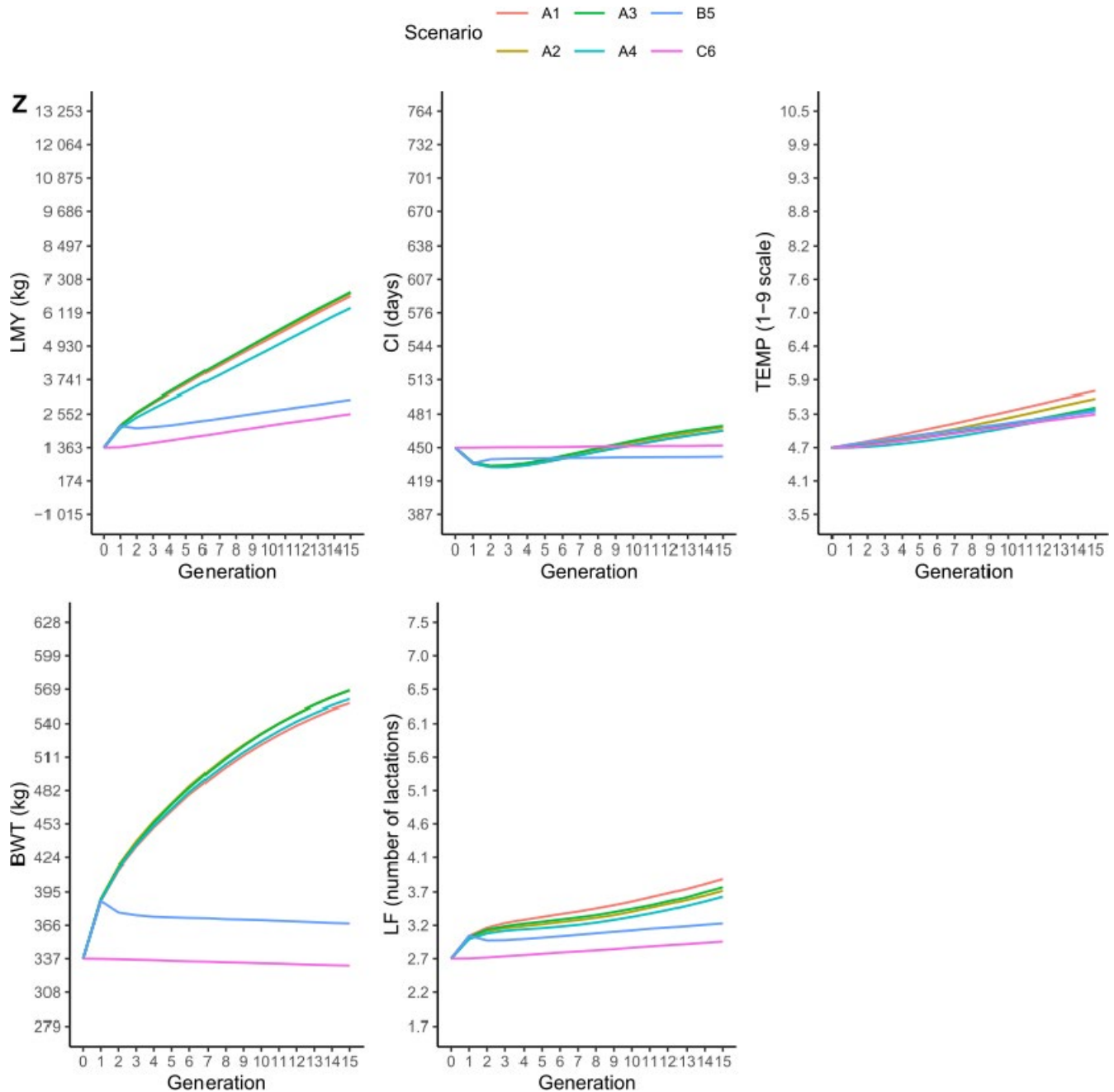
APPENDIX 20

Predicted genetic trends in the Overall Farmer Index at 100% (X), 50% (Y) and 30% (Z) AI schemes when performance of the exotics in sub-Saharan Africa was assumed to be reduced by 25% compared to the base simulation design. Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).



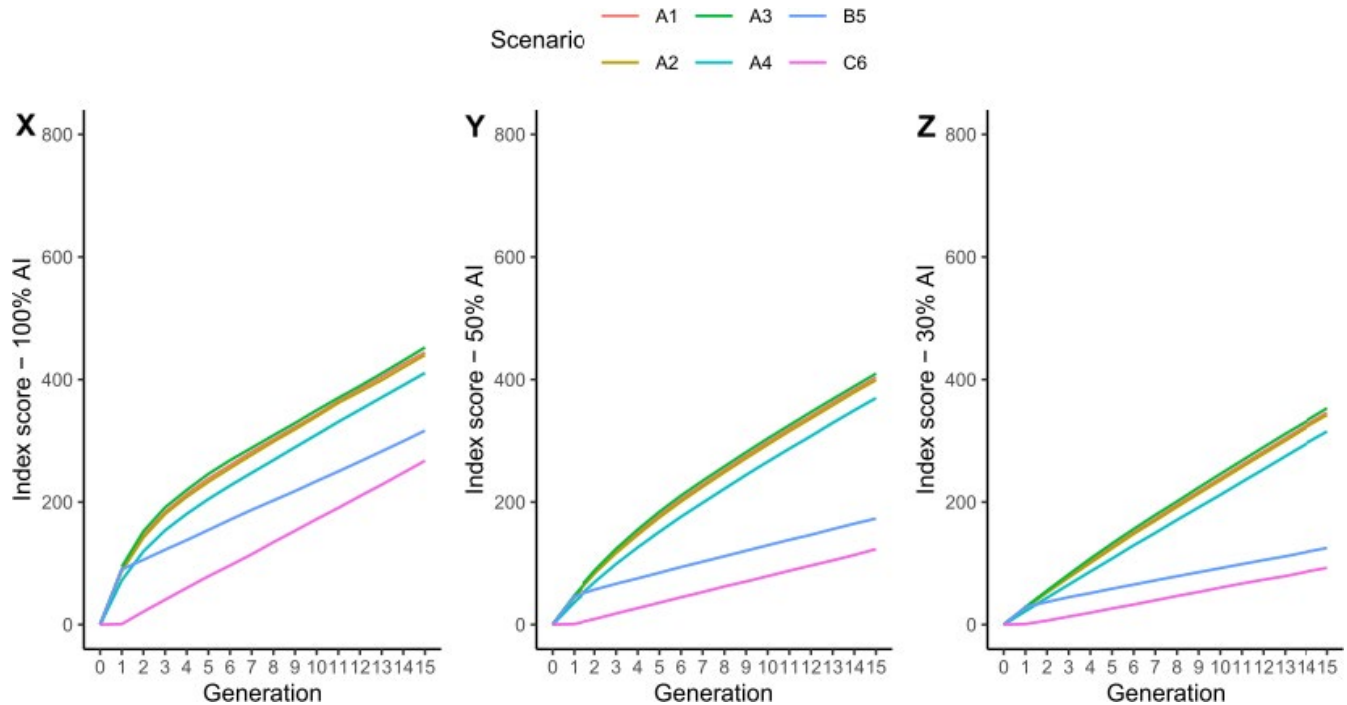
APPENDIX 21

Predicted genetic trends for individual animal traits at 100% (X), 50% (Y) and 30% (Z) AI schemes when performance of the exotics in sub-Saharan Africa was assumed to be reduced by 25% compared to the base simulation design. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

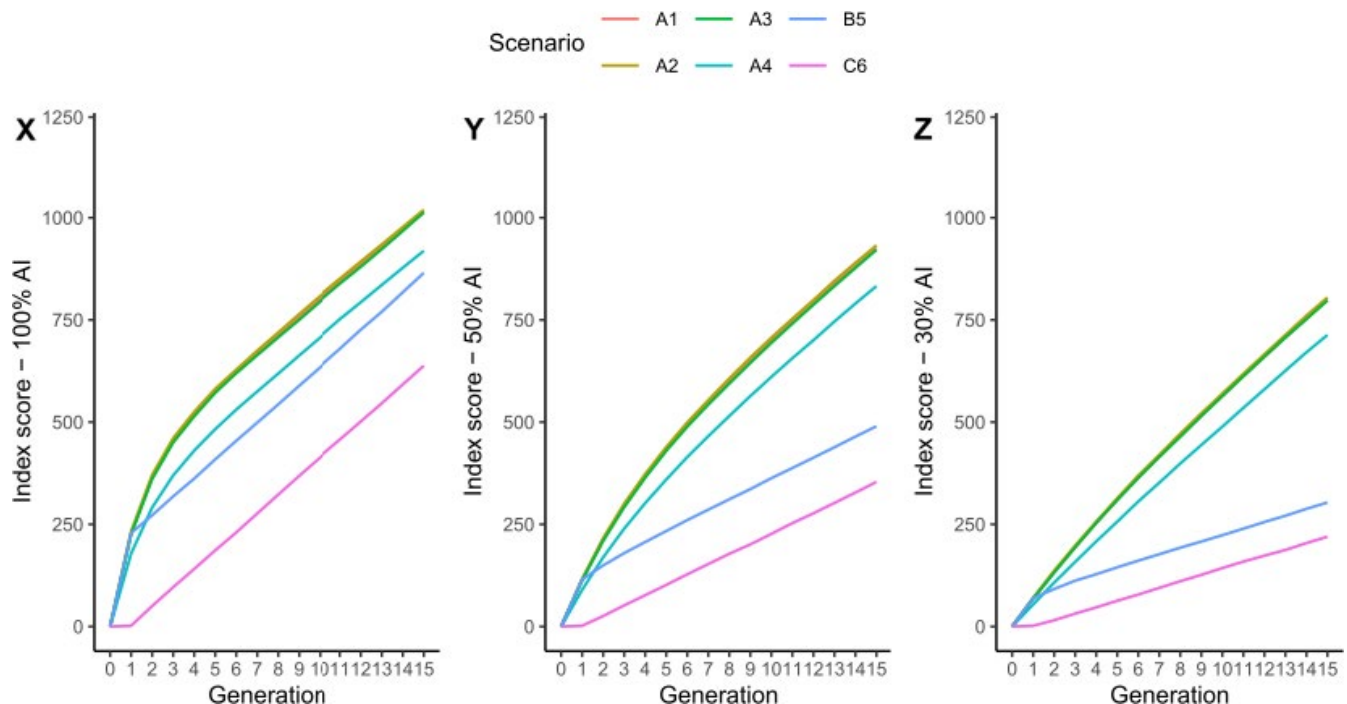


APPENDIX 22

Predicted genetic trends in the Overall Farmer Index in the semi-temperate agro-ecological zone at 100% (X), 50% (Y) and 30% (Z) AI schemes when performance of the exotics in sub-Saharan Africa was assumed to be reduced by 25% compared to the base simulation design. Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).



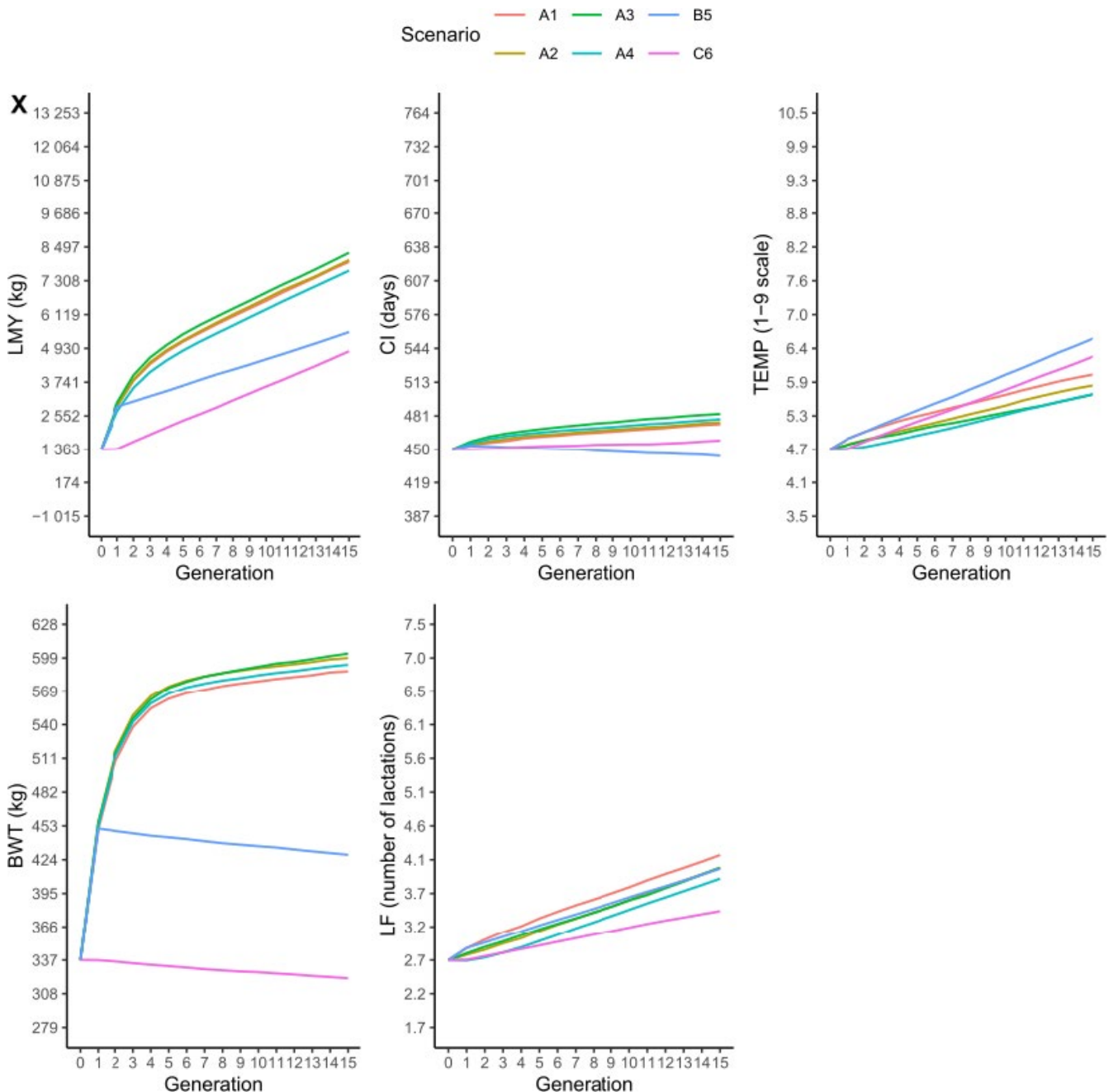
APPENDIX 23



Predicted genetic trends for individual animal traits in the semi-temperate agro-ecological zone at 100% (X), 50% (Y) and 30% (Z) AI schemes when performance of the exotics in sub-Saharan Africa was assumed to be reduced by 25% compared to the base simulation design. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

APPENDIX 24

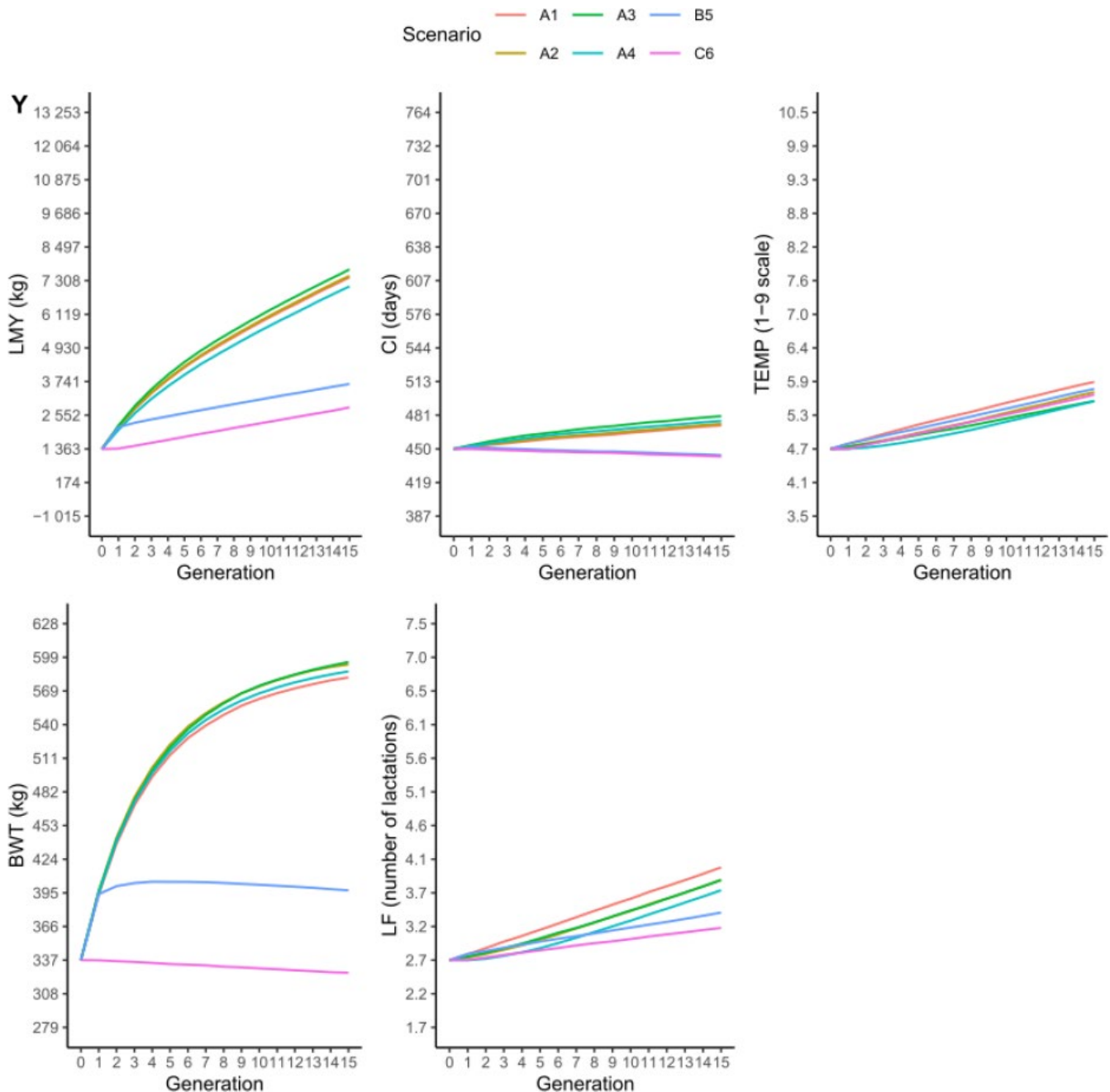
Predicted genetic trends in the Overall Farmer Index in the tropical agro-ecological zone at 100% (X), 50% (Y) and 30% (Z) AI schemes when performance of the exotics in sub-Saharan Africa was assumed to be reduced by 25% compared to the base simulation design. Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer



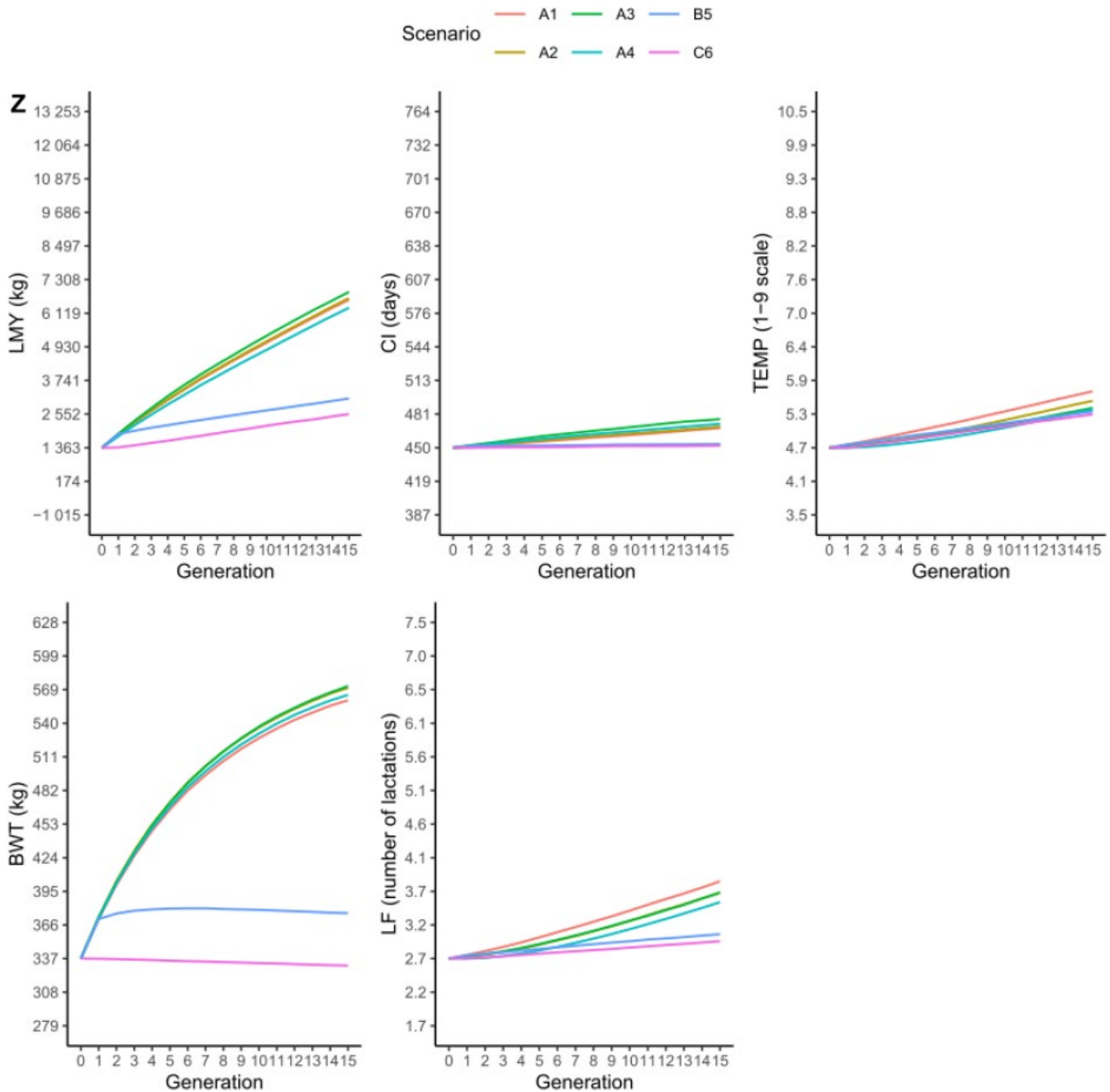
Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

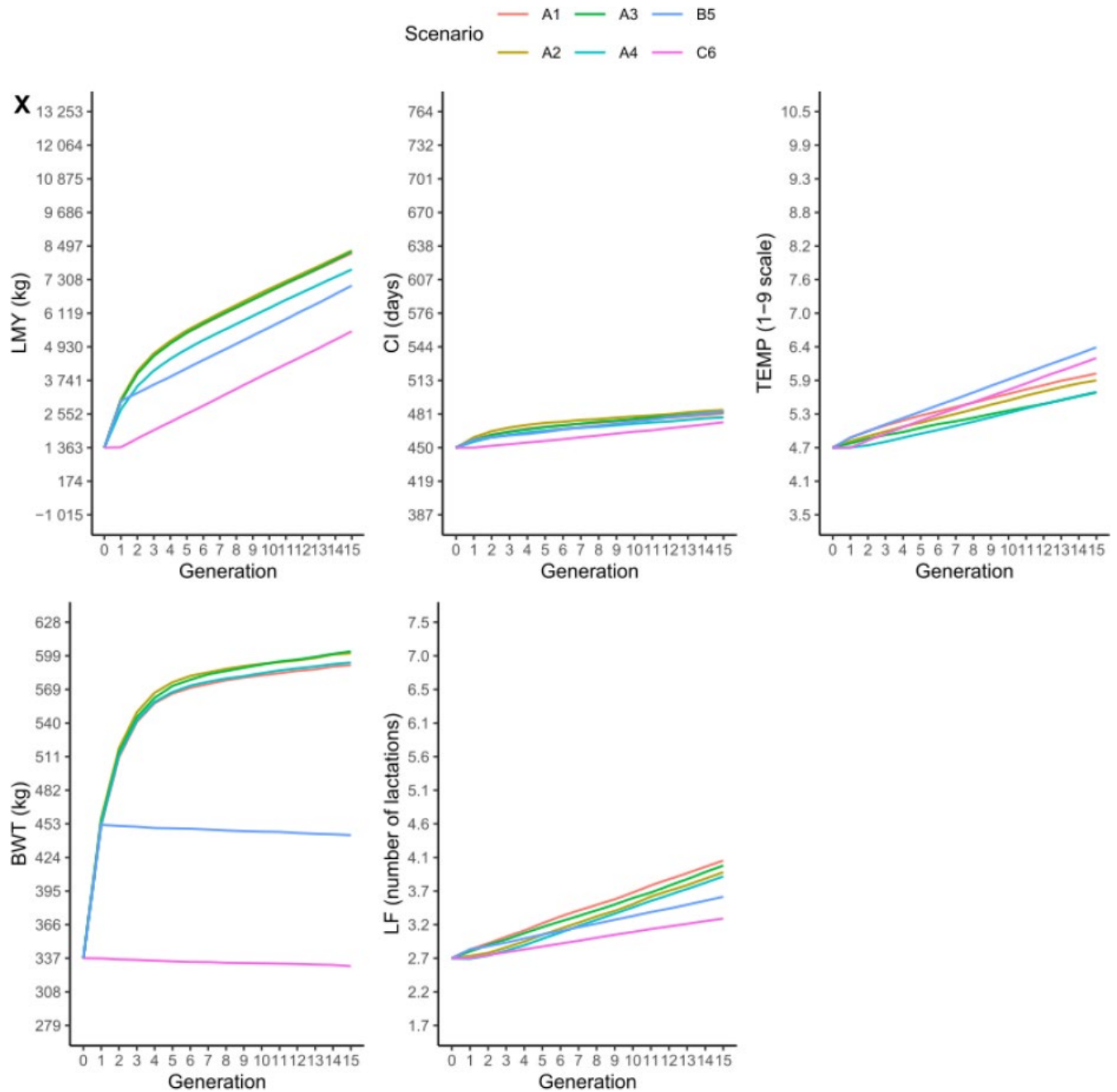
APPENDIX 25

Predicted genetic trends for individual animal traits in the tropical agro-ecological zone at 100% (X), 50% (Y) and 30% (Z) AI schemes when performance of the exotics in sub-Saharan Africa was assumed to be reduced by 25% compared to the base simulation design. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).



Relative differences (%) in predicted genetic gain in individual animal traits and the Overall Farer Index after 15 generations of selection between Scenarios A1 (Importation strategy), B5 (Synthetic breed strategy) and C6 (Indigenous breed improvement strategy); an antagonistic correlation between animal production and fitness (longevity) was assumed combined with reduced fitness of the exotic sires in sub-Saharan Africa. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations).

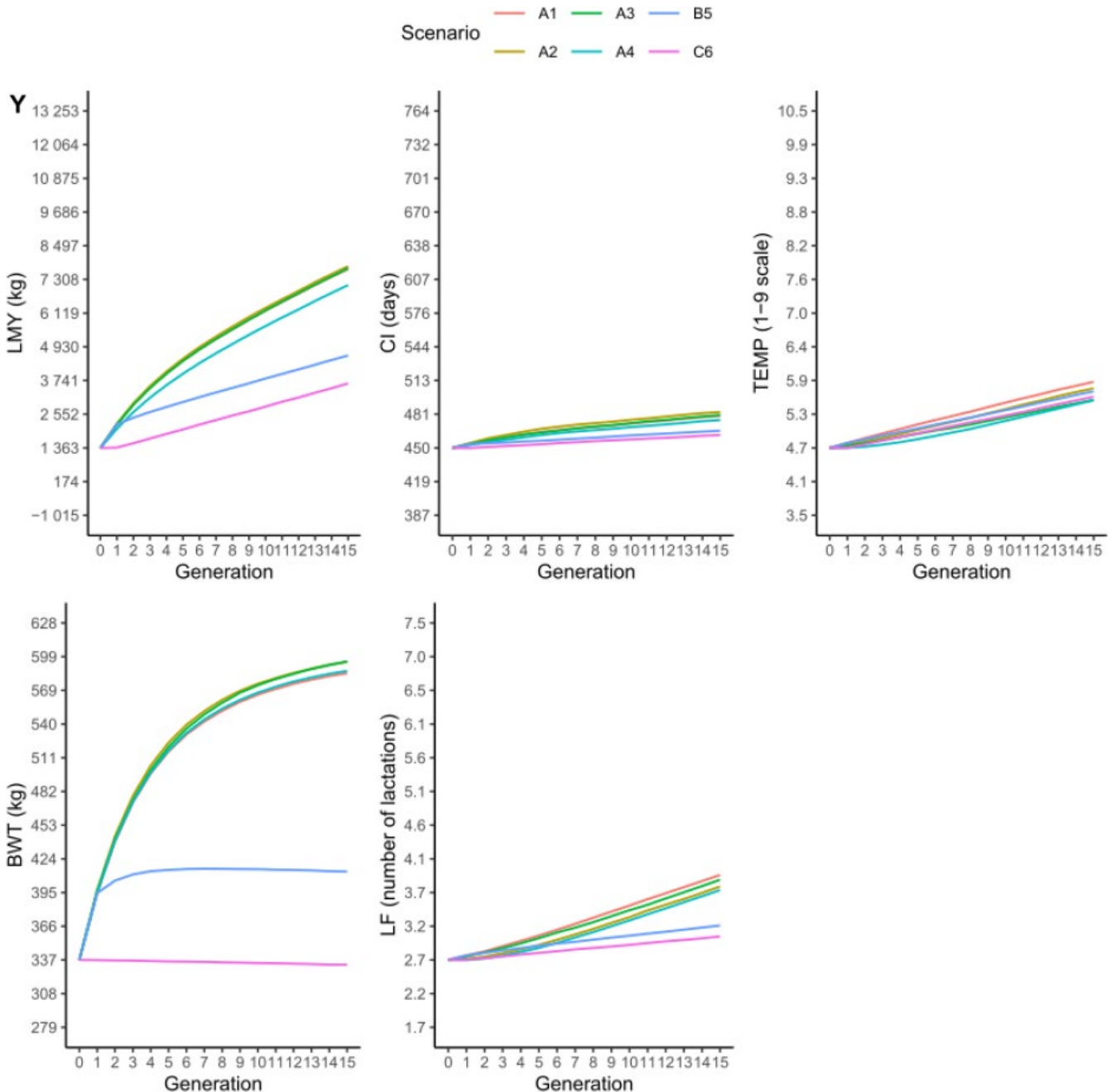




		Difference (%)					Overall Farmer Index
AI-Strategy	Scenario comparison	LMY	CI	BWT	LF	TEMP	
100%	A1 versus B5	13.75%	3.17%	26.43%	26.12%	-15.56%	13.11%
50%	A1 versus B5	40.64%	4.54%	31.33%	21.00%	-3.33%	48.24%
30%	A1 versus B5	51.05%	4.31%	33.25%	16.43%	1.7%3	63.60%
100%	A1 versus C6	35.91%	4.25%	45.44%	19.67%	-12.91%	37.57%
50%	A1 versus C6	53.32%	5.02%	43.58%	16.80%	-2.18%	62.16%
30%	A1 versus C6	59.25%	4.47%	40.83%	13.58%	2.37%	72.89%

APPENDIX 26

Predicted genetic trends for individual animal traits at 100% (X), 50% (Y) and 30% (Z) AI schemes when an antagonistic correlation between animal production and fitness (longevity) was assumed combined with reduced fitness of the exotics in sub-Saharan Africa. LMY = milk yield (kg) in a 305-day lactation (kg); CI = calving interval (days); TEMP = temperament score (1–9 scale); BWT = mature live body weight (kg); LF = longevity (number of lactations). Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).



APPENDIX 27

Predicted genetic trends in the Overall Farmer Index at 100% (X), 50% (Y) and 30% (Z) AI schemes when an antagonistic correlation between animal production and fitness (longevity) was assumed combined with reduced fitness of the exotics in sub-Saharan Africa. Scenarios A1–A4 pertain to imported sires selected based on the Overall Farmer Index, the Reduced Farmer Index, the Exotic Index and randomly, respectively (Strategy A); Scenario B5 pertains to sire selection based on the Overall Farmer Index within a new synthetic breed strategy (Strategy B); Scenario C6 pertains to sire selection based on the Overall Farmer Index within the indigenous cattle population (Strategy C).

